Food provisioning in a generalist predator: selecting, preparing, allocating and feeding prey to nestlings in the Eurasian kestrel (*Falco tinnunculus*)

Byttedyrleveranse hos en generalistpredator: Valg, preparering og allokering av byttedyr og mating av unger hos tårnfalk (*Falco tinnunculus*)

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Abstract

Prey handling behaviour is important for prey selection, but are poorly known for raptors. Therefore, selection and handling of prey by European kestrels (*Falco tinnunculus*) was studied by observing prey transfer outside the nest and by video monitoring prey delivery and prey handling in the nest. Of the prey items recorded delivered by the kestrels to their nests, voles were by far the most abundant prey by number and mass, followed by birds, shrews and then lizards (*Zootoca vivipara*). Insects and frogs were rare. The delivery rate of each of the four types of small mammal prey (shrews, bank vole, *Microtus* voles and wood lemming) increased with increasing abundance of the same prey type around the nest as assessed by snap trapping. The delivery rate of avian prey declined with increasing vole abundance, as did also the delivery rate of shrews, whereas the delivery rate of lizards declined with increasing shrew abundance and increased with increasing mean daily temperature. The probability that a prey item delivered at the nest was a lizard, rather than another prey type, increased towards midday, and also increased with increasing ambient temperature. Thus, the kestrels´ capture of lizards may be regarded as a functional response, where the availability of lizards is determined by solar height and ambient temperature. Mates captured prey of the same size. Females apparently delivered larger prey at the nest, but this was an artefact caused by the fact that males selectively delivered smaller prey directly to the nestlings and larger prey to the female for further processing and finally feeding of the nestlings. The probability of a prey item being decapitated prior to delivery at the nest increased with prey body mass for voles and birds, and decreased with nestling age for voles, but not for birds. No lizard and very few shrews were decapitated prior to delivery. In an average brood each nestling was estimated to consume 67.8 g^{-d}. Daily rate of prey mass delivered was highly associated with nestling age, with a maximum occurring when the nestlings were 17 days old, which was close to the predicted age of 15 days when the growth of the nestlings settled down. For a given type of prey, the variation in handling time was explained by prey body mass. Larger items were ingested at a higher rate than smaller prey when the female fed nestlings, but not when the nestlings became able to feed unassisted. Taken together, during the second week after hatching, when kestrel nestlings become able to feed on small prey unassisted, smaller prey become more profitable than larger prey, and should thus be included when providing the nestlings. However, the benefits of smaller prey items have to exceed the potential cost of dominant nestlings monopolizing small prey and the cost of keeping up a high feeding rate. The kestrel may select different prey depending on whether the prey is intended for self-feeding or for provisioning nestlings, where it would be more profitable to self-feed on small prey and provision dependent nestlings with larger prey.

Sammendrag

Byttedyrhåndtering er viktig for valg av byttedyr, men er lite kjent for rovfugler. Valg og håndtering av byttedyr hos tårnfalk (*Falco tinnunculus*) ble derfor studert ved felt-observasjoner og ved videoovervåkning av reir. Av de byttedyrene som ble levert på reiret utgjorde smågnagere hovedtyngden både i antall og masse, etterfulgt av fugler, spissmus og firfisle. Leveringsraten for hver av de fire byttedyrtypene av småpattedyr (spissmus, klatremus, markmusgruppen og skoglemen) økte med økende tetthet av samme byttedyrtype i terrenget rundt reiret. For fugler derimot avtok leveringsraten med økende tetthet av små-gnagere, Det samme var tilfelle for spissmus, mens for firfisle avtok leveringsraten med økende tetthet av spissmus og økte med daglig gjennomsnittstemperatur. Sannsynligheten for at en firfisle i stedet for et annet byttedyr ble levert på reiret var størst midt på dagen, og økte med økende temperatur. Følgelig kan tårnfalkens fangst av firfisle betraktes som en funksjonell respons, hvor tilgjengeligheten av firfisle bestemmes av solhøyde og temperatur. Maker fanget byttedyr av samme størrelse. Hunnen leverte tilsynelatende større byttedyr på reiret, men dette var kun en indirekte effekt av hannens selektive levering av små byttedyr direkte på reiret, og levering av større byttedyr til hunnen slik at hun kunne dele opp disse til ungene. Sannsynligheten for at et byttedyr var blitt dekapitert før levering på reiret økte med økende byttedyrvekt for smågnagere og fugler, og med økende alder på tårnfalkungene for smågnagere. Ingen firfisler og ytterst få spissmus var blitt dekapitert i før levering på reiret. I et gjennomsnittskull ble hver unge estimert til å konsumere 67.8 g^{-d}. Daglig leveringsrate for byttedyrmasse hang nøye sammen med ungenes alder, og var maksimal da ungene var ca. 17 dager gamle, hvilket var nær den alderen da veksten begynner å avta. For en gitt byttedyrtype var håndteringstiden forklart av byttedyrets masse. Masse konsumert pr. tidsenhet var større for store enn for små byttedyr når hunnen matet ungene, men ikke når ungene spiste på egenhånd. Når ungene blir i stand til å spise selvstendig i en alder av ca. to uker synes mindre byttedyr å bli mer profitable, og bør inkluderes i dietten. Fordelen ved å levere små byttedyr må imidlertid overstige den potensielle kostnaden ved at en dominant unge monopoliserer et slikt byttedyr og kostnaden knyttet til at foreldrene må ha en høy fangstrate. Antakelig vil tårnfalken velge forskjellig byttedyr avhengig av om den skal spise byttet selv eller om den skal mate ungene med det, hvor det vil være mest profitabelt å spise små byttedyr selv og fore ungene med større byttedyr.

1. Introduction

Parental care in a broad sense involves the preparation of a nest or burrow, egg production, care of eggs or young inside or outside the parent's body, provisioning of young prior to and subsequent to birth, and the care of offspring after nutritional independence (Clutton-Brock 1991). In a more narrow sense, parental care only involves the care of eggs or young separated from the parent's body (Clutton-Brock 1991). Provisioning in the meaning of collection and delivery of materials by parents, such as food to their offspring (cf. Ydenberg 2007), is well studied in birds (Kacelnik et al. 1995, Sætre et al. 1995, Siikamäki et al. 1998, Wright et al. 1998, Grieco 2001, 2002a,b, Blanco et al. 2003, Brodin and Jonsson 2003, Fargallo et al. 2003, Barba et al. 2009). For a parent bird, provisioning involves energy spent to collect and deliver food (Ydenberg 2007) which can affect their own survival and reproductive success (Dijkstra et al. 1990, Daan et al. 1996, Korpimäki and Rita 1996, Blanco et al. 2003). Optimization models of food provisioning assume that a parent behaves so as to maximize the total energy delivered to the nest (Houston 1987, Ydenberg et al. 1994). Provisioning models for birds stress the importance of the parent´s delivery capacity, both in terms of the amount of food delivered to nestlings and the amount needed for self-feeding (Ydenberg 2007).

The potential food delivery is dependent on the provisioner's working capacity and food availability (Ydenberg 2007). In raptorial birds, i.e. hawks (Accipitriformes), falcons (Falconiformes) and owls (Strigiformes), survival and reproduction are affected by the density of potential prey types (Newton 1979). Provisioning parents need to alter their feeding behaviour in relation to prey availability, to provide sufficient food to their nestlings. Accordingly, food provided by parents is found to vary with prey densities (Geer 1981, Sodhi 1993, Bernard et al. 2010). Raptors have been shown to exhibit functional response to voles (Korpimäki and Norrdahl 1991, Sonerud 1992, Korpimäki et al. 1994, Jeschke et al. 2002, Valkama et al. 2002), i.e. they have been found to take more voles in years with higher vole densities. In addition to changes in prey availability on a seasonal or inter-annual scale, short-term changes in environmental conditions, on the scale of hours, may also affect prey selection by raptors. Raptors breeding at southern latitudes often prey upon ectothermic prey, and some to such an extent that they are classified as insect eaters or reptile eaters (Newton 1979). At northern latitudes, reptiles and large insects are less abundant, but some generalist raptors may nonetheless include such prey in their diet (e.g., Gil-Delgado et al. 1995, Selås 2001). For ectothermic reptiles, external heat is required for maintaining an optimal body temperature to maximize physiological functions (cf. Avery 1987). By being dependent on high ambient temperatures for their activity, and thus being more active on warmer days, reptiles may suffer weather-dependent predation risk (Huey and Slatkin 1976). The raptors´ capture rate of reptiles may be regarded as a functional response, where the availability of reptiles is determined by environmental factors (e.g. warm weather).

In most raptors, there are marked sex roles during breeding, with the female performing most or all of the incubation, brooding and feeding of nestlings, whilst the male provides most or all food for the family, assisted by the female in the later part of the nestling period, if at all (Newton 1979, 1986, Cramp and Simmons 1980, Cramp 1985, Wiehn and Korpimäki 1997, Eldegard et al. 2003, Sunde et al. 2003, Eldegard and Sonerud 2010). The different sex roles during the breeding season may subsequently involve differences in prey selection between the sexes. Most raptors take large prey for their size, which may be impossible for nestlings to handle, requiring extended parental assistance for partitioning and feeding (Newton 1979, 1986, Cramp and Simmons 1980, Cramp 1985). The female dismembers the prey and feeds the morsels to the nestlings, staying at the nest or close by, retrieving the items captured by the providing male, and thus relieving him from feeding and allowing him to resume hunting more rapidly (Slagsvold and Sonerud 2007).

Nestling food demand may vary predictably as the nestlings grow (Ydenberg 2007), because older nestlings are larger and require more food than younger nestlings. The nestling growth rate is not constant, and nestlings may need most energy when their growth rate is at the highest (Barba et al. (2009). In altricial birds, parental food provisioning usually increases with nestling age, especially during the phase when the nestlings grow fastest, but provisioning tends to flatten out when nestlings approach their final body mass (e.g. Grundel 1987, Dijkstra et al. 1990, Blondel et al. 1991, Barba et al. 2009). In terms of optimal food provisioning during the breeding season, the parents may alter the selection of prey type and prey size for delivery (Ydenberg 2007).

Prey handling may affect prey selection, and the evolution of prey handling in predators has influenced the evolution of their prey (e.g., Sherry and McDade 1982). Handling time is defined as the sum of capture time, preparation time and ingestion time (e.g., Kaspari 1990). The type of prey affects the time allocated by the parent to capture, prepare, and either self-feed on the prey or provide it for the nestlings. Handling time is a function of prey type and prey size (Salt and Willard 1971, Craig 1978, Griffiths 1980, Paszkowski and Moermond 1984, Kaspari 1990, Diaz and Carrascal 1993, Banbura et al. 1999, Nilsson and Bronmark 2000, Grosch 2003). Further to this, ingestion rate, i.e. prey mass consumed and energy gained per unit handling time, partly determines prey profitability and depends on prey type and prey size (Sullivan 1988, Ille 1991, Grosch 2003, Slagsvold and Sonerud 2007). Studying ingestion rate is an essential step towards understanding prey selection and feeding behaviour. Data on ingestion rate is important for quantitative tests of optimization models (Emlen 1966, Stephens and Krebs 1986, Ydenberg and Hurd 1998), models considering central place foragers, where the parent travels from the hunting patch to the nest with a single prey item or several (Orians and Pearson 1979, Wetterer 1989, Stephens and Krebs 1986), models considering prey size and prey handling as determinants of sex roles and reversed sexual size dimorphism in raptors (Slagsvold and Sonerud 2007), and finally, for this study in particular, models considering food provisioning, where the parents feed dependent nestlings (Houston 1987, Ydenberg et al. 1994).

The aim of this thesis was to investigate how rates of prey delivered to nestlings by parents in the Eurasian kestrel (*Falco tinnunculus*), hereafter termed the kestrel, were affected by the abundance of small mammals within the kestrel territories (PAPER I); whether a reptile, the common lizard (*Zootoca vivipara*), was captured more often during warm conditions (PAPER II); whether parental sex roles influenced the prey captured and delivered by mates (PAPER III); whether some prey items were more prepared prior to delivery at nests than others as a function of prey type, prey size and nestling age (PAPER IV); how much food, in terms of prey mass, was consumed by the nestlings (PAPER V); whether parental effort varied with nestling food demand (PAPER VI) and whether ingestion rate, including when an adult female feeds her nestlings and when the nestlings fed unassisted, varied with prey type and size (PAPER VII). Whether this findings are valid for other raptors are discussed and suggestions for future studies are given. In the concluding section of this thesis I try to give some answers to prey selection by the provisioning kestrel parent during the breeding season.

2. Methods

2.1 Study area and study species

This thesis is based upon video monitoring of adult kestrels providing prey at nests in the boreal and hemi-boreal zones in Trysil municipality in Hedmark county, in south eastern Norway (61º07´-61º32´ N; 11º56´-12º48´ E), in June–July 2003 and 2005–2009 (Fig. 1). The project had access to > 300 nest-boxes, of which c. 150-300 were annually used by breeding kestrels. The nest boxes were situated on solitary trees in clear-cuts and bogs, and the surrounding habitat was typically coniferous forest with a large proportion of clear-cut areas, but negligible patches of agricultural areas. The kestrel is well suited for studying food provisioning for three reasons: i) It has a broad diet, including small rodents, shrews, birds, lizards and insects. ii) It is common and tolerant towards human disturbance, such as video monitoring. iii) It prefers to nest in artificial nest-boxes (Village 1990), and video monitoring works well for identifying prey provided to the nest by the parents (Steen 2009). During the first two weeks of the four weeks nestling period, the male alone provides prey to the female, who then portions it to the nestlings. The female portions the prey until the nestlings are able to feed unassisted, at which point, both the parents bring prey items and leave them to the nestlings (Village 1990, Fargallo et al. 2003). In general nestlings feed unassisted when they are two to three weeks old, however this varies in accordance to prey type. The estimated age above which the nestlings consumed >50% of the prey items unassisted was 12 days for lizards, 14 days for shrews, 19 days for birds, and 20 days for voles (R. Steen, unpublished data).

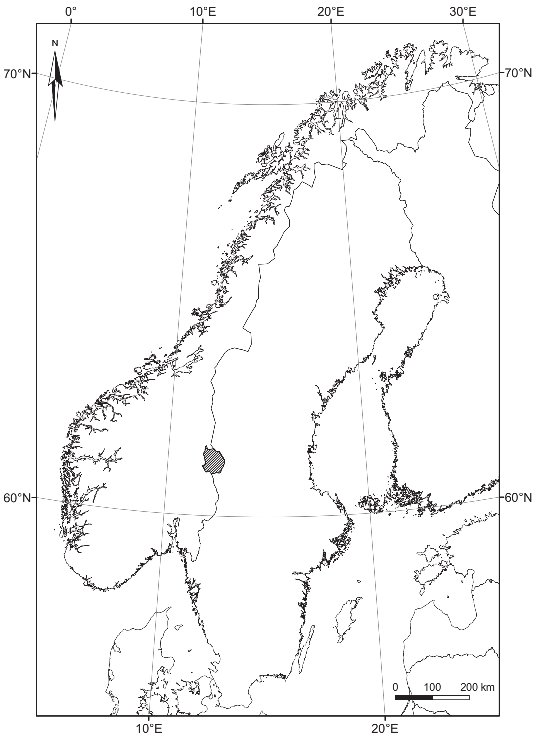

Figure 1. Map of Fennoscandia, with the shaded area showing Trysil municipality in Norway.

2.2 Video monitoring

During the last decade, video technology has rapidly advanced and wildlife video monitoring has successfully been conducted by using modern VHS time lapse, hard disk, and mini digital recorders (e.g. McQuillen and Brewer 2000, Booms and Fuller 2003, Rogers et al. 2005, Reif and Tornberg 2006, Steen 2009). In this study, both continuous and event triggered video recording were used. Video filming enabled a much more precise measurement of the diet and prey mass delivered by the parents, when compared with more traditional analyses, such as studies based on pellet samples or direct observation from a hide (Lewis et al. 2004), see appendix for details.

In total, 55 nests were monitored. These were in 47 different nest boxes; i.e. six nest boxes were filmed for two years and one for three years. Of the nest boxes filmed for two years, three were filmed in subsequent years, one was filmed three years apart, and two were filmed five years apart. The nest box filmed for three years was first filmed two years apart and then three years apart. No brood was abandoned during this study.

Digital video camcorders were used at nine nests in 2003 and ten in 2005. The camcorders were either mounted on the top of the nest box (2003), or placed on the ground and connected to a camera lens in the box through a 50 m modified video cable (2005). In 2006, six nests were monitored using the same nest-box setup as in 2005, but instead of using a camcorder as a recording unit, a time lapse video recorder (VHS) and a hard disk recorder (HDD) in combination with an external camera were used. In 2007 (ten nests), 2008 (eleven nests) and 2009 (nine nests) a small camera was placed in the back corner underneath the roof and pointed towards the entrance of the nest box. The camera was mounted with a wide angle lens to cover a broad view inside the nest box. The camera was connected with a video cable to a mini digital video recorder (mini DVR), which stores data on SD cards (for details see Steen 2009). Different set-ups between years were a consequence of technical improvement, i.e., more efficient installation procedure and easier maintenance. All set-ups were equally capable of recognizing prey items delivered at the nests.

2.3 Video analysis

For each prey delivery, the prey item was identified. Most vertebrate prey items were identified to species or genus, but insects were identified to order. Prey body mass was calculated for the prey deliveries in 2003 and 2005. The body mass of adult birds has a relatively small intra-specific variation, and a mean value for each species was therefore obtained from data most pertinent to the breeding season in Fennoscandia. For passerines, juveniles were assigned the same body mass as adults, whereas for grouse and shorebirds, the body mass of juveniles was estimated from appearance and relative size on the video frame. Insect body mass was taken from a study of the kestrel´s diet in Finland (Itämies and Korpimäki 1987). The body mass of lizards and small mammals has a relatively high intra-specific variation, and was therefore estimated from body size on the video frame (see appendix for further explanation).

During 2003 and 2005, the handling time of each prey item was estimated (measured to the nearest second), when the female fed dependent nestlings and when the nestlings fed unassisted. In the former cases, handling time was defined as the time elapsed from when the female bent her head down to tear off the first piece until the item had been completely consumed or abandoned. If the nestlings fed unassisted, they would either monopolize the prey item or share it with one or more siblings. In these cases, therefore, handling time was taken as the time elapsed from when the nestling lowered its head to tear off the first piece until the item was completely consumed or abandoned, or, if the prey item was swallowed whole, the time elapsed from when the nestling received the item from the parent until its swallowing movements ended. Sibling fights over food were excluded from the feeding time, where possible. If the female or nestlings stopped feeding for longer than 4-5 s, the pause was also excluded from the feeding time.

2.4 Estimating small mammal abundance

The abundance of small mammals in each kestrel territory was estimated in 2007 – 2009.The area surrounding each of the 30 monitored nests were set with 120 snap traps for two consecutive days and nights around the time of filming, yielding a maximum of 240 trap nights per nest. In each of the four cardinal directions from the nest, 30 traps were put out at intervals of c. 10 m. For each trap, the associated habitat was recorded, and for each trapped animal, the associated trap was recorded. In this way, a separate trapping index could be calculated for each species in each habitat, as number of individuals captured per 100 trap nights. Kestrels hunt in open habitats (Village 1990). Therefore, two trapping indices were calculated for each species; one for all habitats, and one for open habitats suitable for hunting kestrels, i.e. excluding data from old and dense forest.

3. Results and discussion

3.1 Prey selection

Of the prey items recorded delivered by the kestrels to their nests, voles were by far the most abundant prey by number and mass, followed by birds, shrews and then lizards. Insects and frogs were rare. The dominance of voles, amongst prey taken by kestrels during the breeding season, corresponds with earlier findings (Yalden and Warburton 1979, Korpimäki 1985, 1986, Kochanek 1990, Village 1990). The mass-specific energy content of insects, frogs, lizards, shrews, voles and birds seems to be quite similar, and also the assimilated portion of the energy content of the prey consumed (Masman et al. 1986, Karasov 1990, Studier and Sevick 1992, Voituron et al. 2002, Tryjanowski and Hromada 2005). Hence, prey mass was assumed to adequately reflect energy delivered.

The delivery rate of each of the four types of small mammal prey (shrews, bank vole, *Microtus* voles and wood lemming) increased with increasing abundance of the same prey type around the nest, as assessed by snap trapping. The delivery rate of avian prey declined with increasing vole abundance, as did also the delivery rate of shrews, whereas the delivery rate of lizards declined with increasing shrew abundance and increased with increasing mean daily temperature. (PAPER I). The probability that a prey item delivered at the nest was a lizard, rather than another prey type, peaked around midday, and increased with increasing ambient temperature (PAPER II). Given that the kestrels responded functionally to the availability of lizards as determined by solar height and ambient temperature, one would assume that during sunny and warm weather, the kestrels would switch foraging tactic to focus on lizards, or to restrict their search effort to microhabitats where lizards are most abundant (cf. Holling 1966).

3.2 Prey allocation and parental effort

Kestrel mates captured prey of the same size. The females apparently delivered larger prey at the nest than the males, but this was an artefact caused by the fact that males selectively delivered smaller prey directly to the nestlings and larger prey to the female for further processing and subsequent feeding of the nestlings (PAPER III). The reason for this size-dependent prey allocation by the male was probably the fact that the nestlings are able to ingest smaller prey unassisted sooner (Sonerud et al. 2010). When parents provide small prey items like insects, lizards and shrews to the nestlings, they have to keep up higher delivery rates, i.e. spend more time hunting, to meet the food demand of the nestlings (PAPER V). Therefore, because the male usually provides most of the prey during the first half of the nestling period (Village 1990, Fargallo et al. 2003), the male may more likely deliver larger prey to the nestlings to compensate for the cost of high delivery rates to meet the nestling food demand. Later on, when the female also hunts (Village 1990, Fargallo et al. 2003), both parents could together deliver more prey per time unit, and the parents may then meet the nestlings food needs even with small prey items. In fact, parents were found to deliver smaller prey items in the later nestling period (PAPER VI). The growth of the body mass of the kestrel nestling saturates and the food demand peaks, when the nestlings are c. 15-17 days old. The kestrel parents were found to have the highest rate of prey mass delivered when the nestlings were 17 days old (PAPER VI). One week later, the delivery rate declined and was equal to that when the nestlings were c. one week old (PAPER VI). This was achieved by a reduced prey item delivery rate and by providing smaller prey items (PAPER VI). As a consequence, one may expect that smaller prey is delivered to the nestlings more often as they grow older and when both parents hunt.

3.3 Handling time and handling mode of prey

When the female kestrel fed dependent nestlings, the efficiency (i.e. ingestion rate) of handling prey in the nest for the brood as a whole was higher for larger than for smaller items of lizards, voles and birds (PAPER VII). This is opposite to what was found for self-feeding raptors of ten species from three avian orders in temporal captivity (Slagsvold and Sonerud 2007, 2010), and may be a consequence of the fact that the female often delivered the morsels from a prey item to more than one nestling, so that feeding may have been less constrained by time spent swallowing. Partitioning of the prey items into smaller pieces may increase food assimilation, but also compete for time needed for other activities, such as brooding, self-feeding and hunting.

When provisioning larger prey, the female would pay a cost by being restricted to the nest to feed the nestlings for a longer period, compared to when provisioning smaller prey that the nestlings would be able to handle by themselves at an earlier age (Sonerud et al. 2010). Hence, the parents may prefer smaller prey to gain an early nestling independence, given that the availability of small prey is high enough to maintain a delivery rate high enough to meet the nestlings´ food demand (PAPERS V and VI). Therefore, the family as a whole may also benefit from parental provisioning of small prey at a relatively early nestling stage. On the other hand, by providing dependent nestlings with small prey items during the first two weeks after hatching, i.e. when only the male hunts, means that the kestrel parents may not be able to maintain a sufficiently high feeding rate to meet the nestlings food demand (PAPERS V and VI). Further to this, if the diet had consisted of mainly small prey items, which are possible to monopolize (i.e. lizards and shrews), a dominant nestling would have obtained more food and developed faster than its siblings. Due to this conflict, the parents may select to deliver larger prey at the nest to avoid an uneven distribution of food among the nestlings. In addition to this, the female kestrel may also prevent a dominant nestling obtaining all food by feeding more of the young from one prey item and also partition small prey despite a longer handling time.

Although the amounts of uneaten remains were not estimated in this study, the general impression was that these were few. Sometimes wings and legs from avian prey remained, but apparently no parts of small mammals were left. However, the proportion of uneaten remains was more likely to be higher for avian prey than for mammalian prey because the former were usually plucked prior to delivery; i.e. a varying portion of the wings, tail and body feathers had been removed (Steen 2004, Løw 2006), and most likely increased with prey size, as found for self-feeding raptors in temporal captivity (Slagsvold et al. 2010). Adjusting ingested mass for uneaten remains would reduce the estimated profitability of larger prey, and in particular avian prey. However, the parents sometime remove the intestines of voles prior to delivery at the nest (Masman et al. 1986). Removal of intestines was not quantified in the present study, but some of the voles delivered had their abdomen opened, indicating that the parent had removed entrails prior to delivery. These voles were excluded from the analysis. However, the cost of removing parts of a vole may be compensated for by the gain of eating the parts; kestrels usually eat the head of prey (Village 1990), and during breeding the female may eat the intestines (Masman et al. 1986). According to own observations, the kestrel female also fed the nestlings with the intestines from voles, and such intestines were never observed as remnants in the nest boxes, in contrast to feathers and legs from avian prey. However, to avoid disturbance, no visit were conducted to the nests to collect and weigh prey remains after each meal.

In addition, if larger prey takes longer to prepare prior to delivery at the nest, for instance due to decapitating or plucking, the ingestion rate of large prey would be overestimated. In fact, the probability that a prey item was decapitated prior to delivery at a kestrel´s nest increased with prey mass (PAPER IV).

3.4. Food provisioning vs. self-feeding

The high ingestion rate of large prey when the female fed the nestlings, and probably a more even distribution of food among the nestlings (PAPER VII), and the high ingestion rate of small prey when adult raptors are self-feeding on small prey (Slagsvold and Sonerud 2007), may lead to the observed pattern that kestrel parents are more likely to consume lizards than voles at the capture site, and more likely to bring voles than lizards to the nest (Sonerud 1989). This also corresponds with the fact that male kestrels are found to deliver larger voles to the female and nestlings than they consume themselves at the capture site (Masman et al. 1986). A different prey selection between self-feeding and provisioning has also been found in rhinoceros auklets (*Cerorhinca monocerata*) and common guillemot (*Uria aalge*), where the parents provided larger prey items to nestlings compared to prey items for self-feeding (Davoren and Burger 1999, Wilson et al. 2004). Ydenberg (1994), Davoren and Burger (1999), and Wilson et al. (2004) points out the importance of discriminating between prey self-feeding and provisioning of nestlings in foraging and life history studies. Hence, there may exist a dichotomy between prey selected by the kestrels for self-feeding and prey selected for provisioning during breeding.

3.5 Raptors in general

The findings present in this thesis may be applicable for other raptorial birds. The benefit of a high ingestion rate for self-feeding parents may play a more important role for raptor species that are more adapted to hunting for prey in flight, because raptors that are hunting agile prey have a fast food passage due to relative small intestines, and as a consequence they have to increase the food passage rate to maintain a maximum digestive efficiency and immediate regain maximum flight performance (Barton and Houston 1993a,b, Barton and Houston 1996). The combination of the need of rapid food passage rate and maximize digestion may select for raptors that efficiently prepare and dismember the prey before swallowing. As a consequence, raptors that usually dismember the prey before swallowing may be more efficient when feeding dependent nestlings (cf. PAPER VII). The effect of prey type and prey size on ingestion rate and food distribution among nestlings may also have implications for the evolution of reversed sexual size dimorphism (RSD) in raptorial birds (cf. PAPER III). When relatively large prey are provided, the female need to partition the prey and feed the nestlings, and would benefit from being large to do this efficiently (cf. PAPER VII). However, for raptors providing relatively small prey, the nestlings would be able to handle their prey unassisted at an early age, and the benefit to the female of being large would be less due to lack of need for food dismembering (Sonerud et al. 2010). Further to this, since the provisioning of small prey items could result in increased competition among the nestlings, where the larger female nestlings would receive more food than the male nestlings (e.g. Anderson et al. 1993, Fargallo et al. 2003), provisioning such prey would select for minimizing the intersexual size difference within the brood in order to minimize the probability of a female-biased sex ratio at independence. Hence, the selection favouring RSD in raptors may be countered by selection to minimise female competitive dominance among nestlings in species providing small prey (Anderson et al. 1993).

3.6 Perspectives for future studies

The diet of raptorial birds seems to be well known. However, previous studies have analysed remnants and pellets from nests and plucking sites (Yalden and Warburton 1979, Korpimäki 1985, 1986, Toyne 1998, Huang et al. 2006). The probability of finding remnants may be lower for smaller prey than for larger prey, and thus the proportion of small prey may have been underestimated (cf. Lewis et al. 2004). Video monitoring of nests is a more exact method to determine the real diet of a raptorial bird (e.g. McQuillen and Brewer 2000, Lewis et al. 2004, Reif and Tornberg 2006, Steen 2009), and represent a major improvement from traditional diet analysis based on pellets and prey remains.

Further quantification of the difference between type and size of prey selected for self-feeding and provisioning to nestlings mentioned above might be possible through field observations of hunting parents (e.g. Masman et al. 1986, Sonerud 1989) in combination with video monitoring of prey delivered at the nest (e.g. Lewis et al. 2004, Rogers et al. 2005, Steen 2009). By combining field observation with video monitoring, it could also be possible to link hunting behaviour with the prey type identified on the video. Hence, it will be possible to see if there is a relationship between the prey type captured and type of habitat used in raptors (cf. Preston 1990, Madders 2003, Thirgood et al. 2003), between prey type and hunting technique (cf. Rijnsdorp et al. 1981, Csermely et al. 1989, Hakkarainen et al. 1992, Csermely and Bagni 2003, Wuczynski 2005), and between prey type and the decision of whether and where to prepare prey before delivering it to nest (cf. PAPER IV).

In cases where prey are spatially and temporally clumped, the chance of making a successful hunting trip may be higher if the predator returns from the central place to the last capture site and waits for a new prey item to appear, than if the predator searches at random (the win-stay search strategy hypothesis; (Sonerud 1985). The combination of field observations and video monitoring may provide data to test a recently developed foraging model that supports the hypothesis based on sparse empirical data (Mitchell and Lima 2002).

When a central place foraging single-prey loader, such as a raptor, gathers food for dependent nestlings, it has to decide between self-feeding and provisioning for the nestlings. Foraging models predict that this decision depends on the size of the prey, and on the distance from the capture site to the nest (Stephens and Krebs 1986). In general, parents should self-feed on smaller prey on the capture site and carry only the larger prey to the nest (Sonerud 1989), and size of prey carried to the nest should increase with increasing distance to the nest (Stephens and Krebs 1986). By combining field observations and video monitoring it would be possible to test whether size of prey delivered at the nest increases with increasing distance from nest to capture site (Stephens and Krebs 1986).

4. Conclusion

Taken together, during the first two weeks after hatching, when the kestrel female has to partition prey and feed dependent nestlings and the male does most of the hunting, the male should select larger prey items for provisioning, and in particular large voles when abundant, to ensure a sufficient delivery rate, a high ingestion rate when the female is feeding dependent nestlings, and an even distribution of food among the nestlings. On the other hand, when the nestlings become able to feed unassisted and swallow small prey whole in the second week after hatching, it would be favourable to include small prey in the diet, i.e. shrews and in particular lizards, because intake rate would then be high for an individual nestling, and because the female would be relieved from prey partitioning and allowed to hunt. However, the density of smaller prey needs to be high to meet the nestlings' food demand, and the benefits of delivering small prey have to exceed the potential costs of keeping up a sufficient feeding rate and the cost of a dominant nestling monopolizing such prey. There may be a difference between the optimal prey type and size selected by the kestrel for self-feeding and for provisioning during breeding, because it seems to be more profitable to self-feed on small prey and provision dependent nestlings with large prey. Further quantification of the type and size of prey selected for self-feeding by the kestrels might be possible through field observations of hunting parents (Masman et al. 1986, Sonerud 1989) in combination with video monitoring of prey provisioned at the nest (Lewis et al. 2004, Rogers et al. 2005, Steen 2009). The findings may be applicable for other raptorial birds as well, and in particular for models considering food provisioning, where the parents feed the dependent nestlings, but also for understanding the different sex roles and the evolution of reversed sexual size dimorphism.

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Appendix

Estimating the body mass of lizards and mammals delivered at the nest by kestrels

The body mass of lizards and small mammals has a relatively high intra-specific variation (Hansson 1992, Yoccoz and Mesnager 1998, Smajda and Majlath 1999, Norrdahl and Korpimäki 2002). Therefore, the body mass of each lizard and small mammal prey item delivered by the kestrels was estimated from the body size on the video frame for the data from 2003 and 2005, rather than using an average mass for each species as has been done in previous studies (Korpimäki and Norrdahl 1991, Fargallo et al. 2003, Laaksonen et al. 2004). Because the estimation of individual prey body mass required the whole body to be exposed, the body mass of some lizards and mammals could not be estimated. To estimate the body mass of the lizards and small mammals that the kestrels delivered at the nests the natural prey was measured on a monitor and compared it with corresponding measurements of prey of known mass. For the measurements a 1:1 model of each nest box was used. Two nests in the first filming period in 2003 were excluded for the measurements of voles and lizards because of unsuitable camera angle. Each nest box model was provided with a grid system in the same plane as the front wall in the nest box, and placed where the expected bill positions of kestrel would appear. Measurements of three stuffed perching kestrels with a prey in their bill were used to estimate bill position, and made a model for these measurements. The grid system would appear through the longitudinal axis of the prey hanging from the kestrel's bill. For each nest box model the camera was placed in the same angle and position as during filming in the field, and then recorded the grid system. This recording was transferred to the software package Pinnacle Studio 8 (2001), and then linked to the original film clip recorded in the field. A transition with a 50% degree of transparency was made between these two clips, making it possible to see both the grid system and the prey item (see fig.2 below). These edited recordings were viewed with a video projector (Epson LCD projector, model EMP 500, 1996). For each recorded mammal the number of grid squares (5 mm x 5 mm) covered by the prey were counted.

This procedure was repeated with 20 small mammals of known body mass; by placing six common shrews *Sorex araneus* (7.3 - 9.6 g), six bank voles *Myodes glareolus* (11.5 - 21.8 g), six root voles *Microtus oeconomus* (7.9 - 47.9 g) and two wood lemmings *Myopus* *schisticolor* (18.2 - 18.9 g) in the bill of the kestrel model for each nest-box, and recorded this on video. The number of grid squares covered by each of the small mammals of known mass was counted, and a relationship between the number of covered grid squares and body mass was calculated. From these measurements a regression line, $f(x) = a + b\ (x^{1.5})$ was calculated, where $f(x)$ is the estimated body mass, and x is number the grids squares covered by the small mammal. For the material in 2003 this had to be done for each nest box separately, because the boxes had different sizes, but in 2005 the ten nest boxes were of the same size so the procedure had to be done only once. There was no significant difference between the regression slopes of different species, so the four species were pooled for each nest box. The number of grid squares covered by the natural prey items was used to calculate the prey body mass, using the regression from their respective nest.

For common lizards (*Zootoca vivipara*), the regression model by Van Damme and Vanhooydonck (2001) was used, $\log_{10}(m) = -1.767 + 3.201 * \log_{10}(SVL)$, where SVL is snout-vent length. From the grid screen the snout-vent length was obtained and by the regression line the body mass of each lizard recorded was estimated. Many of the lizards were delivered without tail, but this was not subtracted from the estimated mass because it proved difficult to quantify the point of refraction, and because no data on the mass of a lizard´s tail was available.

The body mass of birds has a relatively small intra-specific variation; therefore a mean value for each prey species was obtained from data most pertinent to the breeding season in Fennoscandia (Cramp and Simmons 1980, 1983, Cramp 1985, 1988, 1992, Cramp and Perrins 1993, 1994a,b, Matthysen 1998, Selås 2001). If an avian prey was identified to genus only, as for instance many thrushes (*Turdus*) were, an average body mass of the possible species alternatives was calculated. For passerines, juveniles were assigned the same body mass as adults, whereas for grouse and shorebirds, the body mass of juveniles was estimated from appearance and relative size on the video frame. For the birds delivered decapitated, 12.9 % of the body mass was subtracted, based on the relative mass of heads removed by self-feeding raptors handling avian prey in captivity (T. Slagsvold and G. A. Sonerud, unpublished data). Most of the birds were plucked prior to delivery; i.e. a varying portion of the wings, tail and body feathers had been removed. The body mass for this removal was not corrected for, both because it was difficult to make a precise quantification of the mass of plucked feathers, and because this mass is rather minor according to studies of raptors in captivity (T. Slagsvold and G. A. Sonerud, unpublished data).

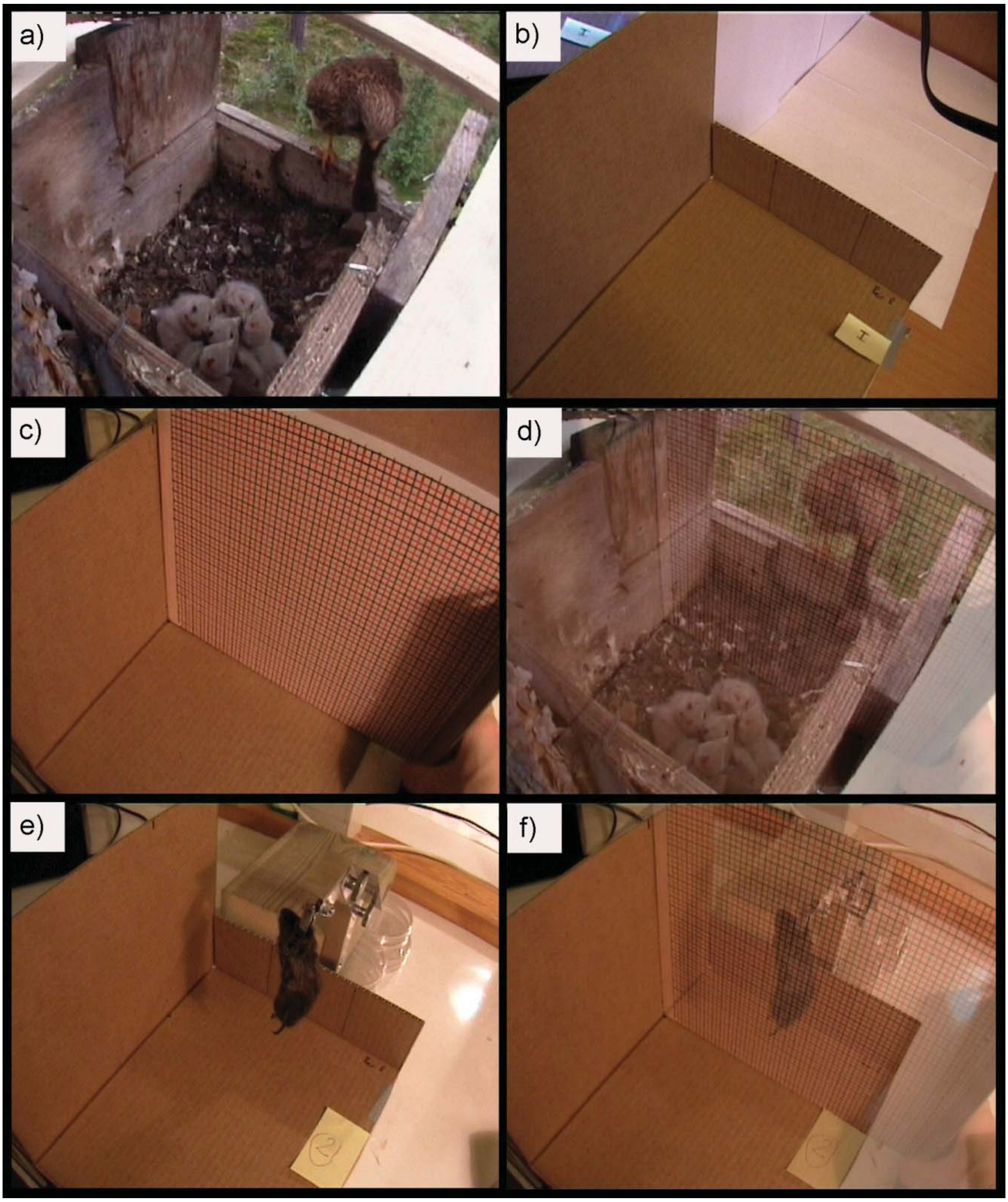

Figure 2. a) A female kestrel with a prey delivered to the nest, filmed in the field. b) A model of the nest box, with the camera in same angle and position as during filming in field. c) The nest box model provided with a grid system placed were the expected bill position of the kestrel would appear. d) The grid system and the prey item with a 50 % degree of transparency. From this the number of grid squares covered by the prey was counted. e) The nest box model with a prey item of known size in the bill of the kestrel model. f) Both the grid system and the prey item of known size with a 50 % degree of transparency. From this the number of grid squares covered by the prey was counted

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Compilation of papers (I-VII)

Paper I

Multi-species functional response in a generalist raptor

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Abstract

Understanding a predator´s functional response is paramount for understanding the effects of the predator on its prey populations, but estimating this relationship in a natural system of wild animals is fraught with methodological challenges. We minimized the problems inherent in previous studies by using video to record all prey deliveries during three days in the nestling period at 30 nests of a generalist raptor, the Eurasian kestrel (*Falco tinnunculus*), and by estimating the abundance of all mammalian prey species by snap-trapping around each of the nests close to the time of filming. For each of the three prey types of voles; bank vole (*Myodes glareolus*), *Microtus* voles and wood lemming (*Myopus schisticolor*), the delivery rate was best explained by a model only including the abundance of that prey type. For the fourth type of small mammal prey; shrews (*Sorex*), the delivery rate was best explained by the abundance of shrews and the abundance of all voles pooled, with a positive and negative effect, respectively, and by nestling age, with a positive effect. Hence, the kestrels seemed to have a non-selective multi-functional response to the small mammals, probably due to the fact that the profitability of these prey types to the kestrels was quite similar as long as the female fed the nestlings. The delivery rate of avian prey was best explained by the abundance of all voles pooled and kestrel brood size, with a negative and positive effect, respectively. Thus, birds were alternative prey to voles for the kestrels, which fits the fact that the profitability of birds was lower than that of voles. The delivery rate of common lizards (*Zootoca vivipara*) was best explained by the abundance of shrews and by mean daily temperature, with a negative and positive effect, respectively. Thus, in the same way as the kestrels captured shrews and voles in proportion to their abundance, the kestrel seemed to capture lizards and shrews in proportion to their abundance, where the functional abundance of lizards to kestrels was mediated by the activity-regulating ambient temperature. This fits the fact that lizards and shrews were the most profitable prey to kestrels when the nestlings became able to consume prey unassisted. Due to the load-size effect in central place foragers, the functional response as estimated from prey deliveries at the nest is biased compared to the real one based on prey captures, but it is probably the best estimate until video cameras can be mounted onboard the predators.

Keywords: Eurasian kestrel, *Falco tinnunculus*, foraging, functional response, load-size effect, prey handling, prey selection, raptor, video

Introduction

Understanding a predator´s functional response, i.e. how the predator´s capture rate is affected by prey abundance (Solomon 1949, Holling 1959), is paramount for understanding the effects of the predator on its prey populations. However, in a natural system of wild animals estimating this relationship is far from straightforward, both because the predator usually exploits populations of several prey species, and because estimating capture rate and prey abundance is fraught with methodological challenges. Therefore, the most precise estimates of functional response in wild animals have been obtained in field experiments, for instance with foraging birds exposed to stationary food items such as fruits or seeds, where the behaviour of the predator have been recorded on a short time scale (e.g. Cresswell 1997, Stillman & Simmons 2006, Smart et al. 2008).

Most studies on functional response have dealt with a predator´s response to a single prey species, either because the predator has been regarded as a specialist (e.g. Nilsen et al. 2009), or because the prey species has been regarded as the major prey of the generalist predator studied (e.g. Salamolard et al. 2000, Vucetich et al. 2002). Even in studies of a generalist predator preying on multiple species, the functional response has usually been estimated for each prey species independent of the others (e.g. Korpimäki & Norrdahl 1991, Rutz & Bijlsma 2006, Millon et al. 2009), with one exception (Redpath & Thirgood 1999, see also Smout et al. 2010). Furthermore, any effects of other factors on the functional response, such as weather conditions or predator group size have only rarely been tested (e.g. Cresswell 1997, Nilsen et al. 2009).

Obtaining a correct measure of capture rate for free ranging predators in natural systems has been very difficult. Therefore, estimates of capture rates have often been based on complex calculations from data representing evidence of prey captures, such as prey remnants or the content in scats or regurgitated pellets, either left by self-feeding predators or accumulated in or near dens or nests of providing predators, resulting in rather coarse and error-prone approximations to real delivery rates (e.g. Korpimäki & Norrdahl 1991, Salamolard et al. 2000, Millon et al. 2009, Nilsen et al. 2009). It has been similarly difficult to obtain a correct measure of the prey density to which the predator is exposed, and estimates based on counting or trapping are likely crude approximations (e.g. Redpath et al. 1995). Moreover, usually only one estimate of prey abundance has been made for a study area housing a population of the predator, so the same estimate of prey abundance has been used for several territorial predator individuals, masking any spatial variation in encounter rates

(Redpath & Thirgood 1999). Also, usually data from all predators studied have been pooled for each year (e.g. Korpimäki & Norrdahl 1991), masking any inter-individual behavioural differences (animal personality *sensu* Wolf et al. 2007, cf. Dingemanse et al. 2007). Taken together, a sample with one data point per year for a population of predators would mask much interesting variation. In addition, because the estimate of prey capture rate is usually based on data accumulated over weeks or months, whereas prey abundance is usually estimated in the course of a few days, the estimates of prey abundance may poorly reflect what the predator encounters. Finally, such studies with a resolution on the scale of years do not allow testing the effect of environmental factors operating on a shorter time scale.

Therefore, knowledge about how short-term changes in environmental conditions on the scale of hours would affect the functional response of predators in general, and raptors (hawks (Accipitriformes), falcons (Falconiformes) and owls (Strigiformes)) in particular is lacking. Because the diet of raptors has been estimated from prey remnants and regurgitated pellets collected at or near the nest during or after breeding, or from prey stored in the nest, analyses of environmental effects has been restricted to an inter-annual scale, as typical for studies of functional response (e.g. Kellomäki 1977, Korpimäki and Norrdal 1991, Reif et al 2001, Millon et al. 2009). Further refinement in temporal resolution has traditionally required direct observations of prey deliveries from a blind near the nest, but this is very time consuming and has therefore rarely been used (e.g. Suomus 1952, Sulkava 1964, Newton 1986, Redpath 1992). Moreover, the opportunity offered by such observations to relate prey selection to environmental factors on a temporal scale of days or hours has rarely been realised (but see Stinson 1980). The recent advent of various video techniques for recording prey deliveries at raptor nests (Steen 2009 and references therein) has allowed a cost-efficient collection of prey delivery data with temporally high resolution (e.g. Selås et al. 2007, Tornberg and Reif 2007). Still, to the best of our knowledge, such data have hitherto not been used to relate inter-individual variation in prey delivery rates to corresponding inter-territorial variation in prey abundance and environmental factors.

We minimized the problems inherent in previous studies of functional response by wild predators in natural systems by using video to record all prey deliveries at each of 30 nests of the Eurasian kestrel (*Falco tinnunculus*) during three days in the nestling period, and by estimating the abundance of all mammalian prey species by snap-trapping around each of the nests close to the time of filming. In this way, we obtained for each kestrel pair a precise estimate of the delivery rate for each prey type, an estimate of the abundance of each small mammal prey type, and an estimate of environmental variables that may affect delivery rates, such as ambient temperature, nestling age and brood size. The Eurasian kestrel, hereafter termed the kestrel, is a relatively small falcon (male body mass c. 200 g) which is particularly well suited for a study of multi-species functional response, because it is a generalist predator with a diet including insects, reptiles, mammals and birds (Village 1990), i.e. prey types with a large variation in body mass and ingestion time (Steen et al. 2010a), and thus a large variation in profitability. Also, kestrels readily use open nest boxes and are tolerant to disturbance, which facilitates recording of prey deliveries and ingestion. We asked 1) whether the delivery rate of each small mammal prey type depended only on its own abundance or also on the abundance of the other small mammal prey types, 2) whether the delivery rate of non-mammalian prey types depended on the abundance of any mammalian prey type, and 3) whether the delivery rate of any prey type was affected by environmental factors. Finally, we related the variation in the kestrels´ response between prey types to the profitability of these prey types to the kestrels.

Methods

The study was conducted in June-July in 2007-2009 within a c. 1000 km^2 area (61°07´-61°31´ N; 12°00´- 12°43´ E) in the boreal and hemi-boreal zones in Trysil municipality, Hedmark county, south-eastern Norway. Here >100 kestrel pairs breed in nest boxes each year, of which we video monitored ten in 2007, eleven in 2008 and nine in 2009. The nests were in 30 separate territories, so we assume that no male or female kestrel was involved in more than one year and treated nest as the statistical unit. The average distance to the nearest other monitored nest was 3.3 ± 0.3 (range 2.3-5.8) km in 2007, 3.5 ± 0.8 (range 1.6-9.9) km in 2008, and 4.2 ± 0.6 (range 2.5-7.9) km in 2009. All nests were in boxes with open front, put up 5-15 m above ground in trees located in bogs, clear-cuts or open forest at altitudes of 300-700 m. The study area is covered by coniferous forest intensively managed by modern forestry techniques, i.e. harvesting by unselective clear-cutting, regeneration by planting, and thinning by selective cutting. The proportion of bogs is relatively high, whereas there is only a negligible area of agricultural land in scattered patches.

Estimation of prey delivery rates

Each nest was continuously monitored for three subsequent days, except for one nest in 2008 where the first and second monitoring day was separated by one day. The monitoring started when brood age (i.e. the age of the last hatched nestling) was 10.8 ± 0.3 (range 8-14) days and ended when it was 13.9 ± 0.3 (range 11-17) days. The rate of prey mass delivery in the 30 nests included in this study and in 25 other kestrel nests filmed in 2003-2006 peaked when the brood age was 17 days (Steen et al. 2010b). Brood age was therefore included as a covariate in the analysis to correct for any effect on prey item delivery rate. During filming brood size was on average 4.5 ± 0.2 (range 2-6), and no nestlings died.

In 2007 and 2008 each of the ten original nest boxes was replaced with a nest box special-made for filming. Inside the nest box a CCD camera was placed in the back corner underneath the roof and pointed towards the entrance of the nest box. The camera was mounted with a wide-angle lens to cover a broad view inside the nest box. The camera was connected with a video cable to a mini digital video recorder (mini DVR), which stores data on SD cards (see Steen (2009) for details of the setup). In 2009 the same equipment was used, but instead of replacing the original nest box with a nest box with camera inside we used a special made camera stand. The camera stand was entered into the original nest box while an observer watched the monitor on the ground to ensure a correct camera view. Different set-ups between years were a consequence of technical improvement, and all set-ups were equally capable of recognizing prey items delivered at the nests.

We watched the video frame on a screen in the lab by use of a projector, and identified each prey item delivered by the kestrels to species if possible. Common shrews (*Sorex araneus*), pygmy shrews (*Sorex minutus*), taiga shrews (*Sorex isodon*) and water shrews (*Neomys fodiens*) were pooled as one prey type because we were unable to separate them unambiguously on the video frame. Almost all shrews delivered were probably common shrews (see below). Field voles (*Microtus agrestis*) and root voles (*Microtus oeconomus*) were pooled as one prey type because many items identified as *Microtus* voles could not unambiguously be identified to species. Grey-sided voles (*Myodes rufocanus*) are rare in our study area and very few were trapped, all in clear-cut areas (see below). Because its diet and behaviour make the grey-sided vole similarly vulnerable to avian predation as *Microtus* voles (Hörnfeldt et al. 1990), because *Microtus* voles also occur in clear-cuts in our study area, and because grey-sided voles were difficult to unambiguously separate from *Microtus* voles on the video frame, we pooled the probably very few grey-sided voles delivered with *Microtus* voles as one prey type. For the purpose of this study, birds and insects were not identified below class level. Thus, we used the following nine prey types in the analysis: shrew (*Sorex* spp. and water shrew), bank vole (*Myodes glareolus*), *Microtus* vole (field vole and root vole, and a few grey-sided voles), wood lemming (*Myopus schisticolor*), lizard (*Zootoca vivipara*), frog (*Rana* spp.), mountain hare (*Lepus timidus*), birds and insects.

In total we recorded 1771 prey deliveries. In 73 of these the parent landed on the nest box with a prey without providing it to the nestlings, and instead flew off with the item. However, in 31 of the cases when a parent departed with the item, it arrived within 30 minutes with apparently the same item, which it then provided to the nestlings. We subtracted these cases to avoid double counting items. Hence, the final sample consisted of 1740 prey deliveries.

We calculated a delivery rate for each prey type, taken as number of items delivered per hour of kestrel foraging, At summer solstice, sunrise and sunset is at 03:31 am and 10:55 pm local summer time (GMT + 2 hours), respectively, in our study area.

The daily period of kestrel foraging was set to 20.5 hours, taken as the average of two estimates from our study. The time span between the earliest prey delivery in the morning by any kestrel and the latest in the evening by any kestrel was 20.8 hours, while the longest corresponding time span recorded for one nest was 20.3 hours. Since we aimed at filming for three days, the standard foraging period was set to 61.5 hours. However, due to logistic constraints this period was shorter in eight nests, and longer in one. The average foraging period was 60.6 ± 0.3 (range 53.9-62.3) hours, in total 1818.8 hours for the 30 nests.

Some mammalian prey items could not be identified to species, and a few not even to familiy, because they were partly hidden under the parent kestrel on delivery. To estimate the delivery rate of each prey type as exactly as possible, such items were distributed on the mammalian prey types (see above) in proportion to the distribution of identified mammalian prey items from the actual nest. Thus, if for instance a prey item was identified as being a *Myodes* vole or a *Microtus* vole, and certainly not a wood lemming or a shrew, it was counted as p bank voles, and $1-p$ *Microtus* voles (incl. grey sided vole), where p is the proportion of items identified as bank vole among prey items from the actual nest identified as bank vole or *Microtus* vole (incl. grey sided vole). Or, if a prey item was identified as a vole, and certainly not a shrew, it was counted as p bank voles, q *Microtus* voles (incl. grey sided vole) and $1-p-q$ wood lemmings, where p and q is the proportion of items identified as bank vole and *Microtus* vole (incl. grey sided vole), respectively, among prey items from the actual nest identified as bank vole, *Microtus* vole (incl. grey sided vole) or wood lemming. Finally, if a prey item was identified as a mammal, it was counted as *p* bank voles, *q* *Microtus* voles (incl. grey sided vole), *r* wood lemmings and *1-p-q-r* shrews, where *p*, *q* and *r* is the proportion of items identified as bank vole, *Microtus* vole (incl. grey sided vole), and wood lemming, respectively, among prey items from the actual nest identified as bank vole, *Microtus* vole (incl. grey sided vole), wood lemming or shrew.

The foraging success of a raptor may depend on the weather conditions (Lehikonen et al. 2009), which may either affect the exposure of prey and thus the encounter rate, or it may affect the attack success of the raptor. In particular, the probability that a prey item delivered at a kestrel nest in our study was a lizard increased with ambient temperature and solar height (Steen et al. 2010c). Therefore, we calculated the average daily mean and maximum temperature and the total precipitation for the four days covered by the filming at each nest; when the filming started on day *d* and ended on day *d+3*, we extracted data for day *d* through *d+3*. The data were obtained from Trysil Vegstasjon official meteorological station, situated central in our study area (61°29' N, 12°27' E, at 360 m elevation), and on average 16.2 ± 1.0 (range 3.8-26.5) km from the nest boxes we filmed (n=30). Here, ambient temperature is recorded four times per day (01.00 am, 07.00 am, 01.00 pm and 07.00 pm local summer time (GMT + 2 hours)). The mean and maximum daily temperature averaged 13.4 ± 0.4 (range 10.4-17.8) °C and 19.7 ± 0.5 (range 15.5-25.6) °C, respectively, for the 30 filming periods, and the amount of rain averaged 13.6 ± 2.0 (range 1.2-45.2) mm.

Estimation of prey abundance

To estimate the abundance of small mammals in each kestrel territory, the area surrounding each nest was set with 120 snap traps for two consecutive days and nights, yielding a maximum of 240 trap nights per nest. The traps were permanently baited with cocoa fat (commercial brand “Delfia matfett”). The nest was chosen as origin and 30 traps were put out at intervals of c. 10 m by pacing in each of the four cardinal directions. The positions of the nest and the outermost trap in each direction were recorded by use of a GPS receiver. On average, each trap line covered 383 ± 14 m (n = 120), with no significant difference between the four cardinal directions ($F_{3,116} = 0.32$, p = 0.81). In comparison, average home range (95% MCP) for the males at three of the nests studied in 2008 was 1.87 km^2 (Løken 2009), equivalent to a radius of 772 m if regarded as circular. When hunting, these males, which were radio-tagged after the end of filming, were located on average 695 m from their nest (Ø.

Løken, unpublished data). Thus, our trap lines covered a substantial central part of a kestrel ´s home range.

The traps were set from two days before to 19 days after the filming started, on average 8.2 ± 1.1 days after. This deviation was due to logistic constraints, and was included as a covariate in the analysis to correct for any effect of changes in small mammal abundance between filming and trapping.

The traps were checked the first morning after being set out and collected on the second day. The position of each trap containing a trapped animal was recorded by use of the GPS receiver. For each trap released due to other causes than a trapped small mammal 0.5 trap nights were subtracted. A trapping index was calculated for each small mammal prey type (see above) as number of individuals captured per 100 trap nights. To correct for trap saturation, the number of trap nights was adjusted by subtracting 0.5 trap nights for each individual of other small mammal prey types than the one in question, and by subtracting *n-1* trap nights for *n* trapped individuals of the prey type in question. For each trap, the associated habitat was recorded, and for each trapped animal, the associated trap was recorded. In this way, a separate trapping index could be calculated for each species in each habitat.

Kestrels forage in open habitats (Village 1990), and are able to locate the presence of voles by recording radiation from vole scent marks in the UV-spectrum (Viitala et al. 1995, Koivula et al. 1999). The three radio-tagged males studied in 2008 preferred foraging in bogs with scattered trees and in clear-cuts, often perching in the edges, and avoided old and dense forest (Løken 2009). Therefore, we calculated two trapping indices for each small mammal prey type; one for all habitats, and one for open habitats regarded as suitable for foraging kestrels, i.e. excluding data from old and dense forest.

A total of 751 small mammals were trapped; 97 common shrews, 5 pygmy shrews, 3 taiga shrews, 3 water shrews, 422 bank voles, 6 grey-sided voles, 111 *Microtus* voles (field voles and root voles pooled) and 104 wood lemmings. Thus, an average of 25 small mammals were trapped in each kestrel territory.

Statistical analysis

Statistical analyses were performed with the software JMP® version 5.0 (SAS 2002) and the software R version 2.11.1 (R Development Core Team 2010). First, we performed univariate non-parametric correlations between the non-transformed delivery rates and trapping indices, because these did not have a normal distribution. Second, we used a linear model in the lm package in R (Pinheiro & Bates 2000), and tested separately for each prey type (i.e. shrews, bank vole, *Microtus* voles, wood lemming, birds and lizard) if there was a change in delivery rate as a function of the trapping indices of shrews, bank vole, *Microtus* voles and wood lemming. The response variable was thus delivery rate, and explanatory variables were the trapping index of each small mammal prey type, nestling age, brood size, daily average mean temperature, daily maximum temperature, daily average rainfall and the interaction term between prey trapping index and brood size. For these tests, the delivery rates and the trapping indices were $\log_{10}$-transformed to obtain approximate normal distributions and improve the linear fit (cf. Cresswell 1997). Zero-values were substituted with a small value in the following way. For kestrel nests where no item of a prey type was recorded delivered, the delivery rate for this prey type was set to one half of the rate obtained if one item had been delivered; i.e. the rate obtained if the filming had been twice as long and one item had been delivered. Therefore, since the estimated average activity period for the kestrels during filming was 60.6 hours (see above), we substituted zero values with a delivery rate of 0.00825 items per hour. Correspondingly, for territories where no individual of a small mammal prey type had been snap-trapped, the trapping index was set to one half of the index obtained if one individual had been trapped, i.e. the index obtained if we had used twice as many traps and one individual had been trapped. Therefore, since we used 120 traps for two nights, we substituted zero values with a trapping index of 0.21 individuals per 100 trap nights.

We were seeking the most parsimonious model, i.e. model that gave the best fit with as few explanatory variables as possible. Therefore, different combinations of the explanatory variables were tested, where the model with the lowest $\mathrm{AIC_C}$-value was selected (Burnham & Anderson 1998). We kept to a model when the differences in $\mathrm{AIC_C}$ were larger than 2.0 between this and other models (Burnham 2002). For the selected models we checked for heteroscedasticity by visual inspection of the residual scatter plot (Cook 1994, Tsai et al. 1998), and could state that the variance of residuals was approximately constant, i.e. confirming homoscedasticity. Normal quantile-quantile plot was used to for checking normality of the residuals of the models, by plotting the empirical quantiles of the data against corresponding quantiles of the normal distribution (Becker et al. 1988). The quantiles of the data matched closely the normal quantiles, and the points on the plot fell close to the xy-line for all selected models. The values of the intercept and the slope and the associated 95% confidence intervals were calculated from the lm parameter estimates, using the function "predict.lm" in R (R Development Core Team 2010). In all tests n=30. Mean and standard error is presented as mean ± SE.

Results

Small mammal abundance

The populations of the different small mammal prey types did not fluctuate synchronously during our three years study (Figure 1). In 2007 shrews, bank vole and *Microtus* voles were relatively abundant while wood lemming was scarce. In 2008, *Microtus* voles and wood lemming were relatively abundant, while bank vole was at a medium level and shrews were relatively scarce. In 2009, shrews were at a medium level, while bank vole, *Microtus* voles and wood lemming were scarce. Grey-sided voles were very scarce in all three years. Thus, we obtained a wide range of combinations of abundance of the four small mammal prey types between the territories.

The trapping indices of the small mammal prey types varied independently between the kestrel territories, except in the following cases. Including all habitats, the trapping index of shrews was positively correlated with that of bank vole ($r_s = 0.40$, $p = 0.027$) and negatively with that of wood lemming ($r_s = -0.50$, $p = 0.0046$), and the trapping index of bank vole was positively correlated with that of *Microtus* voles ($r_s = 0.61$, $p = 0.0003$). When restricting the data to open habitats suitable as foraging habitats for the kestrel, the trapping index of shrews was negatively correlated with that of wood lemming ($r_s = -0.53$, $p = 0.0028$), and the trapping index of bank vole was positively correlated with that of *Microtus* voles ($r_s = 0.62$, $p = 0.0003$). Note that the trapping index of shrews was independent of that of all vole species pooled, both when including data from all habitats ($r_s = 0.27$, $p = 0.16$) and when restricting the data to open habitats ($r_s = 0.02$, $p = 0.90$).

Rates of prey items delivered

The total number of items estimated delivered was 1740, constituting 143.3 shrews, 432.4 bank voles, 763.2 *Microtus* voles (incl. grey-sided voles), 61.2 wood lemmings, 183 birds, 90 lizards, 9 frogs, 57 insects, and 1 mountain hare. This corresponds to an average of 58.0 ± 3.3 (range 21-89) prey items delivered at each nest. Average delivery rate was 0.95 ± 0.05 (range 0.37-1.45) prey items per hour (n=30). Frogs and insects were recorded delivered at four nests only, and were therefore excluded from the further analysis, as was also the mountain hare.

For all small mammal prey types, the rate of items delivered at a kestrel nest increased with the abundance of the prey type in the kestrel territory as estimated by trapping. When data from trapping in all habitats were used, the relationship was highly significant for bank vole ($r_s = 0.80$, $p < 0.0001$, Figure 2c), *Microtus* voles (incl. grey-sided vole; $r_s = 0.75$, $p < 0.0001$, Figure 2e) and wood lemming ($r_s = 0.65$, $p < 0.0001$, Figure 2g), but not for shrews ($r_s = 0.22$, $p = 0.25$, Figure 2a). When we restricted the trapping data to open habitats regarded as suitable for foraging kestrels, the relationship improved and became almost significant for shrews ($r_s = 0.36$, $p = 0.052$, Figure 2b), improved marginally for *Microtus* voles (incl. grey-sided vole; $r_s = 0.79$, $p < 0.0001$, Figure 2f) and wood lemming ($r_s = 0.67$, $p < 0.0001$, Figure 2h), and became marginally weaker for bank vole ($r_s = 0.77$, $p < 0.0001$, Figure 2d). Thus, the kestrel showed a functional response to all four small mammal prey types.

The rate of shrews and of non-mammalian prey types delivered at a kestrel nest decreased with increasing abundance of voles (all species pooled) in the kestrel territory. When trapping data from all habitats were used, the relationship was highly significant for birds ($r_s = -0.60$, $p = 0.0005$, Figure 3c), and significant for shrews ($r_s = -0.45$, $p = 0.012$, Figure 3a) and lizard ($r_s = -0.37$, $p = 0.043$, Figure 3e). When trapping data were restricted to open habitats regarded as suitable for foraging kestrels, the relationship remained highly significant for birds ($r_s = -0.64$, $p < 0.0001$, Figure 3d) and shrews ($r_s = -0.51$, $p = 0.0043$, Figure 3b), but became non-significant for lizard ($r_s = -0.30$, $p = 0.11$, Figure 3f).

Factors affecting the rate of prey items delivered

To test which factors that best explained the delivery rate of each small mammal prey type, we used general linear modelling with delivery rate as response variable and the trapping index of each small mammal prey type as explanatory variables. We also included variables that may have an additional effect on delivery rate; viz. total precipitation and average daily mean and maximum temperature during the four days covering the filming, brood size and age of the oldest nestling when filming started, and the date when filming started. In the case of shrews and non-mammalian prey types, we also ran alternative tests where we substituted the three separate trapping indices of bank vole, *Microtus* voles and wood lemming with one trapping index of all voles pooled. We ran separate tests for trapping indices in all habitats and trapping indices in open habitats assumed to be suitable for foraging kestrels.

The delivery rate of shrews was best explained by a model including the trapping index of shrews in open habitats, the trapping index of all vole species pooled in open habitats, and nestling age (Table 1). The delivery rate of shrews increased with increasing abundance of shrews and increasing age of nestlings, and decreased with increasing abundance of voles (Figure 4a).

The delivery rate of bank vole was best explained by a model including only the trapping index of bank vole in all habitats (Table 1). The delivery rate of bank vole increased with increasing abundance of bank vole (Figure 4b).

The delivery rate of *Microtu*s voles (probably including some grey-sided voles) was best explained by a model including the trapping index of *Microtus* voles and grey-sided vole pooled in open habitats, and the brood size (Table 1). The delivery rate of *Microtus* voles (incl. grey-sided vole) increased with increasing abundance of *Microtus* voles (incl. grey-sided vole) and increasing brood size (Figure 4c).

The delivery rate of wood lemming was best explained by a model including only the trapping index of wood lemming in open habitats (Table 1). However, an alternative model with a similar fit (diff. $AIC_c = 0.855$) included only the trapping index of wood lemming in all habitats. The delivery rate of wood lemming increased with increasing abundance of wood lemming (Figure 4d).

Thus, for each of the four small mammal prey types, the delivery rate was solely or partly explained by the abundance of the same prey type in the kestrel territories. For the three vole prey types; bank vole, *Microtus* voles, and wood lemming, the delivery rate was independent of the abundance of the other vole prey types and of shrews. For shrews, however, the delivery rate depended not only on the abundance of shrews, but also on the abundance of all vole species pooled.

The delivery rate of avian prey was best explained by a model including the trapping index of all vole species pooled in open habitats and the brood size (Table 1). The delivery rate of avian prey items decreased with increasing abundance of voles and increased with increasing brood size (Figure 4e).

The delivery rate of lizard was best explained by a model including the trapping index of shrews in all habitats and the daily mean temperature (Table 1). The delivery rate of lizard decreased with increasing abundance of shrews and increased with increasing temperature (Figure 4f).

Discussion

Shrews appeared to be alternative prey to voles for the kestrels in our study, because the delivery rate of shrews declined with increasing abundance of voles in a univariate non-parametric analysis. A corresponding relationship was found for kestrels in Finland; the proportion by body mass of shrews in pellets from kestrels was lower in years with higher vole abundance (Korpimäki & Norrdahl 1991). However, in our study the delivery rate of shrews also increased with increasing abundance of shrews in a univariate non-parametric analysis. In fact, both shrew abundance and vole abundance was included in the most parsimonious model of variables explaining the delivery rate of shrews, with a positive and negative effect, respectively. The estimated age above which the kestrel nestlings involved in the present study consumed >50% of the prey items unassisted was 14 days for shrews and 20 days for voles (R. Steen et al., unpublished data). Thus, during our filming most voles were partitioned by the female and fed to the nestlings, whereas almost half of the shrews were handled by the nestling unassisted. The ingestion rate was c. 40% higher for voles than for shrews when being fed by the female (7.4 vs. 5.3 g^{-min}; Steen et al. 2010a), but prey handling prior to delivery was much more frequent for voles than for shrews; 52% of the voles were delivered decapitated compared to only 1% of the shrews (Steen et al. 2010d). In addition, some of the voles had their intestines removed prior to delivery, and this was never the case for shrews. Thus, assuming that the attack success was similar when the kestrels were aiming at voles and shrews, the profitability of voles and shrews was quite similar. Hence, the kestrels would be expected to attack any shrew and vole encountered. This would result in shrews being taken more with increasing abundance of shrews and less with increasing abundance of voles, as observed. In Scotland, kestrel pellets containing remnants from shrews were more frequent in a year with low vole abundance, in spite of shrew abundance being unchanged, a pattern explained by prey capture in relation to relative and not absolute abundance of voles and shrews (Village 1982). In Finland, experimental removal of avian predators, mainly kestrels and Tengmalm´s owls (*Aegolius funereus*), increased the abundance of shrews when the vole population declined, but not when it increased (Norrdahl & Korpimäki 2000). This fits our finding that kestrels captured more shrews with declining vole abundance.

For each of the three types of vole prey; bank voles, *Microtus* voles (including grey-sided voles) and wood lemming, the delivery rate increased with, and was best explained by, the abundance of the same prey type. Thus, the kestrels had a functional response to each of the vole prey types separately. A corresponding relationship was found for voles taken by kestrels in farmland in Finland; the proportion by prey body mass of *Microtus* voles in pellets from kestrels was higher in years with higher abundance of *Microtus* voles (*M. agrestis* and *M. epiroticus* pooled). For bank vole the corresponding relationship was positive, but not significant (Korpimäki & Norrdahl 1991). For wood lemming Korpimäki & Norrdahl (1991) presented no data, probably because this species was rare in their farmland-dominated study area. Functional responses to all small mammal prey types suggest non-selective multi-functional response, implying that the relative frequency of prey types among prey delivered reflects relative prey abundance (Holt & Kimbrell 2007).

Because the ingestion rate of kestrel nestlings probably does not differ much between different types of vole prey, the kestrels would be expected to attack any vole encountered. This would result in each species being taken more with increasing abundance, as observed. However, the vulnerability to kestrels may differ between the vole species, because their agility and thus their probability of escaping when being attacked is likely to differ (cf. Nishimura & Abe 1988). Voles of the genus *Microtus* are folivorous with well-developed digestive system, in contrast to bank voles, which are less folivorous and have smaller intestines. Grey-sided voles are more similar to *Microtus* voles than to the bank vole in this respect. Therefore, *Microtus* voles and the grey-sided vole would be less agile than the bank vole. Thus, at the same prey abundance, kestrels probably capture more individuals of *Microtus* voles and the grey-sided vole than of the bank vole. We would expect the slope of the relationship between capture rate and true prey abundance to be steeper for *Microtus* voles and the grey-sided vole than for bank vole. In real data, this interspecific difference between the slopes would be even greater due to the fact that the folivorous *Microtus* voles and grey-sided vole is less attracted to baited snap-traps in general, and our cocoa fat baited snap-traps in particular, than the bank vole (G. A. Sonerud, pers. obs.). Village (1990) noted a corresponding difference between voles (mainly field voles) and mice (*Apodemus* spp.), which fits well with the fact that Nishimura & Abe (1988) found Ural owls (*Strix uralensis*) to capture a higher proportion of available individuals of *Microtus* voles than of the more agile *Apodemus* mice.

Birds appeared to be alternative prey to voles for the kestrels in our study, because the delivery rate of birds declined with increasing abundance of voles in a univariate non-parametric analysis. A corresponding relationship was found for kestrels in Finland; the proportion by mass of birds in pellets from kestrels was lower in years with higher vole abundance (Korpimäki & Norrdahl 1991). In fact, vole abundance was included in the most parsimonious model of variables explaining the delivery rate of birds, which also included the brood size, with a negative and positive effect, respectively. Because the estimated age above which the kestrel nestlings involved in the present study consumed >50% of avian prey items unassisted was 20 days (R. Steen et al., unpublished data), most avian prey was partitioned by the female and fed to the nestlings during our filming. The same was the case for voles, and the ingestion rate of birds and voles for the brood as a unit when fed by the female was also quite similar (7.5 vs. 7.4 g^{-min}; Steen et al. 2010a). However, avian prey were handled for a longer time than voles prior to delivery. Firstly, birds were decapitated to a higher extent than were voles; among the prey items recorded delivered at the nest by kestrels in our study area in 2003, 2005 and 2007, 64% of the birds and 52% of the voles had been decapitated prior to delivery (Steen et al. 2010d). Secondly, birds were plucked prior to delivery at the nest (Steen 2004, Løw 2006), and this plucking was estimated to take a similar amount of time as the feeding of the nestlings, hence doubling the handling time and halving the post-capture profitability (G. A. Sonerud et al., unpublished data). The handling of voles prior to delivery at the nest apart from decapitating was negligible compared to the plucking of birds. Thirdly, the attack success of raptors in general, and kestrels in particular, is lower when aiming at birds than when aiming at voles (Temeles 1985, Village 1990), so the kestrel would have to spend more time capturing an avian prey than capturing a vole. An exception may be attacks on fledglings. Thus, for kestrels the overall prey profitability is lower for birds than for voles. Therefore, according to optimal foraging models the kestrels should take birds only when the abundance of voles declines below a critical threshold. According to our data (Figure 3), in eight of the nine cases when the delivery rate of avian prey exceeded 0.1 per hour, the vole trapping index were below 1.4, whereas in 21 of the 22 cases when the vole trapping index exceeded 2.5, the delivery rate of avian prey was lower than 0.1 per hour. Thus, in our study the critical threshold vole abundance for switching to foraging on avian prey was c. 2 voles per 100 trap nights.

Assume that the profitability is higher for voles than for avian prey, and that a kestrel can choose between voles and birds, with energy contents E_V and E_B, and handling times h_V and h_B, respectively, and that $E_v/h_V > E_B/h_B$. Then, according to foraging theory (Stephens & Krebs 1986), when the kestrel does not provide food for the mate or offspring, it should always take voles when encountered and include birds only if the encounter rate for voles is too low. If prey items are sequentially encountered, the kestrel should include avian prey items if the encounter rate with voles declines below a threshold, whereas if prey items are simultaneously encountered, as would be the case with avian prey occurring on the ground among voles in certain habitat patches, the kestrel should include avian prey if the encounter rate with such vole patches declines below a threshold (Stephens & Krebs 1986). When providing prey to the nest for mate or offspring, kestrels bring only one food item each time. We may therefore apply central place foraging theory for single-prey loaders (Stephens & Krebs 1986). With our assumptions, this theory predicts that the kestrel may take only voles if the travel time is short, be unselective for intermediate travel times, and take only avian prey at long distances from the nest (see fig. 3.4 B in Stephens & Krebs 1986). When vole abundance is low, the kestrels would have to forage farther from the nest and would therefore take more birds, i.e. the vole abundance threshold for including avian prey in the diet would become higher.

Due to logistic constraints we were unable to estimate the abundance of birds, so we can only speculate as to whether it would have affected the kestrels´ delivery rate of avian prey. Hen harriers (*Circus cyaneus*) preying mainly on field voles, meadow pipit (*Anthus pratensis*) and red grouse (*Lagopus lagopus scoticus*) chicks had higher delivery rates of grouse chicks with higher grouse density, higher delivery rate of meadow vole with higher meadow vole density, and higher delivery rate of meadow pipit with higher meadow pipit density (Redpath & Thirgood 1999). Since both the hen harrier and the kestrel are generalist predators, their response to changes in the abundance of avian prey probably would be similar.

Apparently, lizards were alternative prey to voles for the kestrels in our study, because the delivery rate of lizards declined with increasing abundance of voles in a univariate non-parametric analysis, although this relationship was significant only when trapping data from all habitats were included. However, vole abundance was not included in the most parsimonious model of variables explaining the delivery rate of lizards, which included the abundance of shrews in all habitats and daily mean or maximum temperature, with a negative and positive effect, respectively. The positive effect of temperature on the delivery rate of lizards fits with the finding based on data from 55 kestrel nests over six years, including the nests in the present study, that the probability of a prey item delivered at a kestrel nest being a lizard rather than another type of prey increased with increasing ambient temperature (Steen et al. 2010c). The reason was probably that lizards become more active with increasing ambient temperature, either foraging or shuttling between shaded and sun-exposed habitat patches, making them more available to kestrels (Steen et al. 2010c). Because the estimated age above which the kestrel nestlings involved in the present study consumed >50% of lizards and shrews unassisted was 12 and 14 days, respectively (R. Steen et al., unpublished data), the nestlings handled slightly more than half of the lizards and slightly less than half the shrews unassisted during our filming. The ingestion rate of lizards and shrews for the brood as a unit when fed by the female was also quite similar (5.3 vs. 4.8 g^{-min}; Steen et al. 2010a), while it was higher for lizards than for shrews when the nestlings consumed them unassisted (21.1 vs. 4.5 g^{-min}; Steen et al. 2010a). None of these prey types required much handling prior to delivery (Steen et al. 2010d). The negative effect of shrew abundance on the delivery rate of lizard may be explained by the fact that lizards and shrews were the two most profitable prey types for the kestrels during our filming because the nestlings could feed on them unassisted, relieving the female from feeding and allowing her to hunt. Hence, the kestrels probably attempted to capture any lizard and shrew when available, but may have focused less on lizards when shrews were abundant.

In four of the six best models, the delivery rate was explained by the trapping index from open habitats regarded as suitable for foraging kestrels. One of the two exceptions was the best model for the bank vole. This species usually occurs at higher densities in forest than in open habitats. In our study, the bank vole populations in dense and old forest may have acted as a source for the bank vole populations occurring in open habitats, where the kestrels foraged. Also the wood lemming occurs at higher densities in forest than in open habitats, and it is noteworthy that the model including the trapping index in all habitats had a similar fit as the model including the trapping index in open habitats (diff. $AIC_c < 2$). The other exception was the best model for the lizard, which included the trapping index of shrews for all habitats. Almost all shrews trapped were common shrews, which occur in all habitats, so that the populations in dense and old forest may have acted as source for the populations in open habitats where the kestrels foraged.

The kestrels had a functional response to voles in our study, while the delivery rates of lizards, shrews and birds were inversely related to vole abundance. Thus, following the terminology of Sonerud (1992), voles were the primary prey of the kestrels, while birds, lizards and shrews were alternative prey. The estimated mean body mass of prey delivered at kestrel nests in our study area were 5 g for lizards, 10 g for shrews, 20 g for voles, and 38 g for birds (Steen et al. 2010d). The size distribution of prey items delivered at a raptor´s nest may be a biased estimate of the size distribution of prey items captured by the raptor, because allocation of prey for transport to the nest among those captured may not be random. In fact, raptors in general tend to carry larger prey to the nest and consume smaller at the capture site (the “load-size effect”; Sonerud 1992 and references therein). The kestrel in particular has been found to consume a higher proportion of lizards than of larger prey at the capture site (Sonerud 1989). Thus, the proportion of lizards among prey items delivered by the kestrels in our study was most likely lower than the proportion of lizards among prey items captured. This underestimation was also probably the case for shrews, although to a smaller extent because they are larger than lizards, but smaller than voles. Moreover, according to the models presented by Sonerud (1992), the magnitude of this underestimation would depend on the abundance of voles. As long as the capture rate of voles, as a type II functional response, is below a threshold, all prey consumed at the capture site would be lizards and shrews (cf. Fig. 1a in Sonerud 1992). Above this threshold, where fewer lizards and shrews are taken than is needed by the hunting kestrel to fulfil its own energy requirement, voles would make up an increasing frequency of prey consumed. Thus, our estimate of the delivery rate of voles would be less biased as the capture rate of voles increases, both in itself and relative to that of lizards and shrews.

Correspondingly, the proportion of birds among prey items delivered by the kestrels in our study was most likely higher than the proportion of birds among prey items captured, because among the prey items delivered birds were larger than voles. Moreover, according to the models presented by Sonerud (1992), the magnitude of this overestimation would depend on the abundance of voles. As long as the capture rate of voles, as a type II functional response, is below a threshold, all voles captured would be consumed at the capture site, and none would be delivered at the nest (cf. Fig. 2a in Sonerud 1992). Above this threshold, where more voles are taken than is needed by the hunting kestrel to fulfil its own energy requirement, voles would make up an increasing frequency of prey delivered. Thus, our estimate of the delivery rate of voles would be less biased as the capture rate of voles increases, both in itself and relative to that of birds.

If we had been able to record all prey items captured by our kestrels, and not only those delivered at the nest, we would have been able to estimate the real functional response curve for the kestrels´ predation on voles. If the alternative prey were smaller than voles, as in the case of lizards and shrews, the real curve would have been below the recorded one for all values of vole abundance, but most so for the lowest values and least for the highest. If the alternative prey were larger than voles, as in the case of birds, the real curve would have been above the recorded one for all values of vole abundance, but most so for the lowest values and least for the highest. Because alternative prey smaller and larger than voles made up a similar number of items in the our study; 233 and 183 respectively, the bias in the estimate of the functional response curve of voles due to the load-size effect probably cancelled out. Moreover, also factors other than the load-size effect may influence the allocation of captured prey for consumption at the capture site or transport to the nest, decreasing the difference between the real functional response curve and the one estimated from prey deliveries at the nest (Sonerud 1992, Korpimäki et al 1994).

The implications of the reasoning above for the capture rate of alternative prey as a declining function of vole abundance are that for lizard and shrews the real slope would be steeper than the recorded one based on delivery rate, whereas for birds the real slope would be less steep. Note that because the delivery rate of shrews was positively related to shrew abundance, and because the delivery rate of lizard was inversely related to shrew abundance, the kestrels also may be regarded to have a functional response to shrews with lizards as alternative prey. Following the reasoning above, the real functional response curve for shrews would have been below the recorded one, most so at low shrew abundance. Also, the capture rate of lizards as a declining function of shrew abundance would have been steeper than the recorded one based on delivery rate.

Our study represents an improvement of previous ones on functional response in natural systems for several reasons. First, our estimates of prey delivery rates based on video recording at the nest are precise and thus better than corresponding previous estimates based on direct observations from a hide, which inherently led to a high proportion of delivered prey remaining unidentified, or only identified to a higher taxonomical level (Redpath & Thirgood 1999). Certainly, our estimates were much more straightforward and less prone to errors than those based on analysis of prey remnants and the contents of pellets or scats (e.g. Korpimäki & Norrdahl 1991, Millon et al. 2009). Second, studies of generalist predators with multi-species functional response are very few (Redpath & Thirgood 1999, see also Smout et al. 2010), and our study represents an improvement, partly because the delivery rate was estimated more accurately, but more importantly because the prey abundance was estimated for each breeding pair separately, thus avoiding the masking of inter-individual variation by pooling data for several nests. Third, our study is the first one to include estimates of the profitability of each prey type, which is needed for interpreting the functional response (see Holt & Kimbrell 2007). The recent advent of video techniques has made it possible to efficiently and precisely estimate prey delivery rates at the fixed point of central place foragers, such as nests of raptors (Steen 2009). However, to estimate the real capture rate of predators in natural systems, the video camera would have to be mounted onboard the predator itself. With the rapid development in camera miniaturization and wireless data transfer, such data collection will probably be achievable in the near future (Rutz et al. 2007).

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Table 1. Factors affecting the delivery rate of prey types at kestrel nests. The trapping indices reflect prey abundance in kestrel territories, either in all habitats, or only in open habitats assumed to be suitable for foraging by kestrels (see text for further explanation). Parameter estimates are for the final GLM model. The delivery rates and the trapping indices are log-transformed. Covariates are not transformed.

Explanatory variable	Estimate	SE	t	R^2	AIC_c	P
Shrew delivery rate						
Intercept	-2.551	0.556	-4.587			<0.0001
Shrew index open habitats	0.460	0.160	2.879			0.0079
Voles index open habitats	-0.337	0.111	-3.035			0.0054
Nestling age	0.130	0.050	2.604	0.489	39.227	0.0150
Bank vole delivery rate						
Intercept	-1.194	0.085	-14.085			<0.0001
Bank vole index all habitats	0.655	0.108	6.078	0.569	33.315	<0.0001
Microtus voles delivery rate						
Intercept	-1.408	0.212	-6.652			<0.0001
Microtus voles index open hab.*	0.500	0.107	4.674			<0.0001
Brood size	0.175	0.046	3.769	0.702	16.794	0.0008
Wood lemming delivery rate						
Intercept	-1.631	0.068	-24.089			<0.0001
Wood lemming index open hab.	0.544	0.115	4.696	0.441	25.829	<0.0001
Bird delivery rate						
Intercept	-1.496	0.208	-7.206			<0.0001
Vole index open habitats	-0.605	0.092	-6.576			<0.0001
Brood size	0.144	0.049	2.930	0.617	17.638	0.0068
Lizard delivery rate						
Intercept	-2.614	0.502	-5.213			<0.0001
Shrew index all habitats	-0.581	0.170	-3.422			0.0020
Daily mean temperature	0.080	0.037	2.161	0.354	36.893	0.0397

* Including grey-sided vole

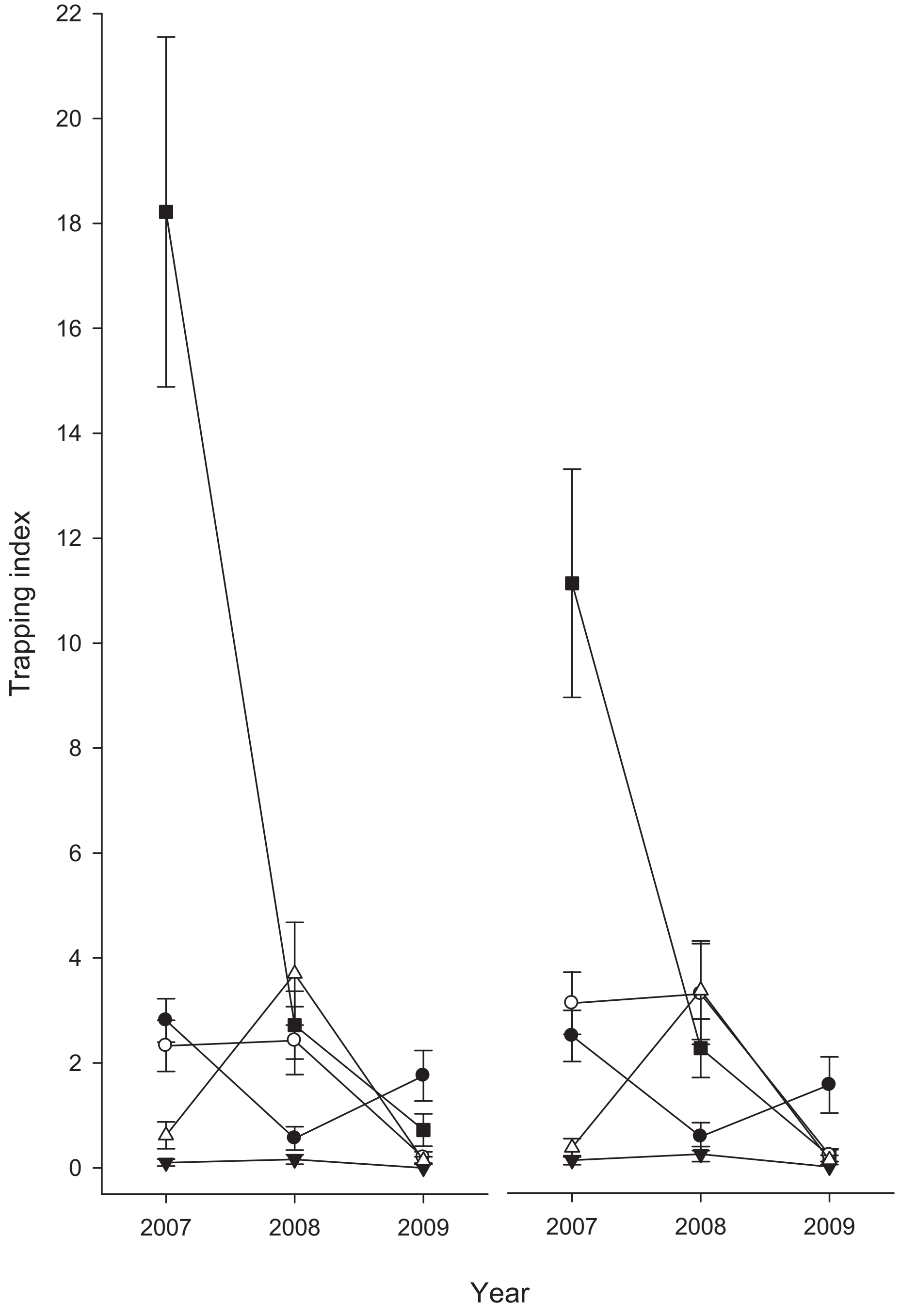

Figure 1. The abundance of small mammals in the kestrel territories in 2007 (n=10), 2008 (n=11) and 2009 (n=9), shown as average (± SE) trapping index, for trapping in all habitats (left panel) and for trapping in open habitats regarded as suitable for foraging kestrels (right panel). Shrews are denotes by filled circles, bank vole by filled squares, *Microtus* voles (field voles and root voles pooled) by open circles, grey-sided vole by filled triangles, and wood lemming by open triangles. See text for calculation of trapping index.

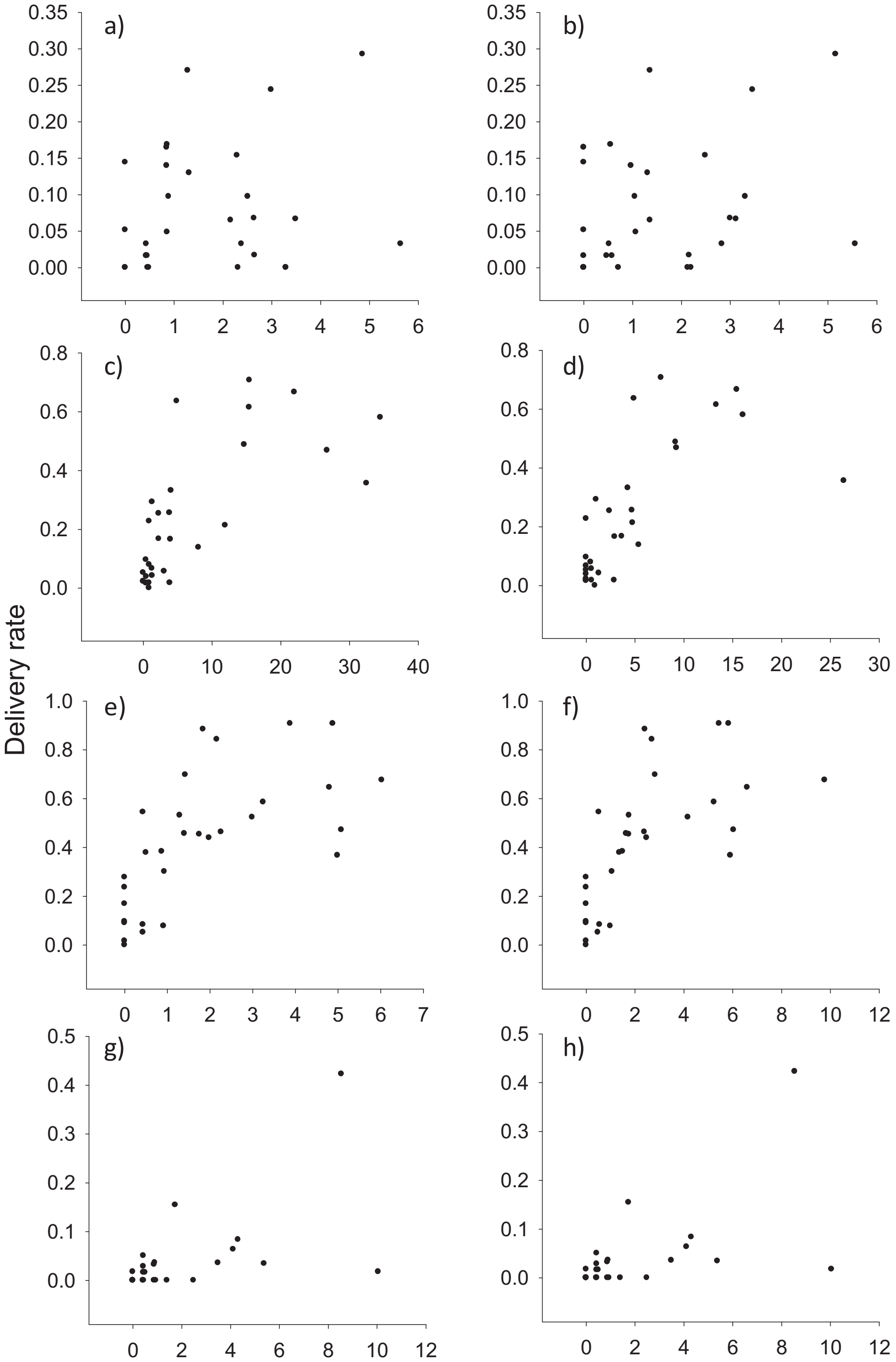

Figure 2. Rate of delivery of a prey type at a kestrel nest in relation to the abundance of the prey type in the kestrel territory, when abundance is based on trapping in all habitats (left column), and when abundance is based on trapping in open habitats regarded as suitable for foraging kestrels (right column), for shrews (a-b), bank vole (c-d), *Microtus* voles and grey-sided vole pooled (e-f) and wood lemming (g-h).

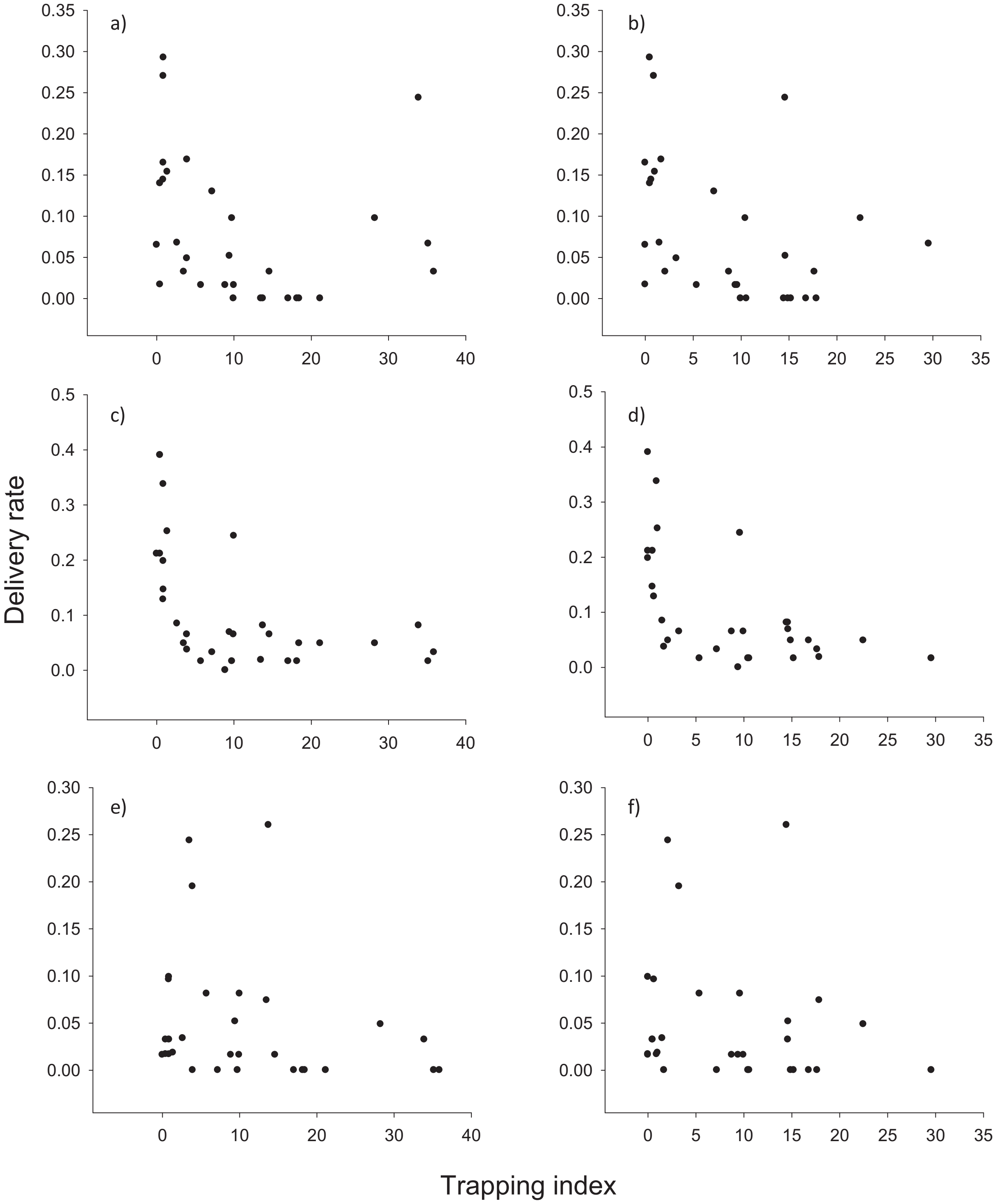

Figure 3. Rates of delivery of non-mammalian prey types at kestrel nests in relation to the abundance of voles in the kestrel territory, when abundance of voles is based on trapping in all habitats (left column), and when abundance of voles is based on trapping in open habitats regarded as suitable for foraging kestrels (right column), for shrews (a-b), birds, (c-d) and lizard (e-f).

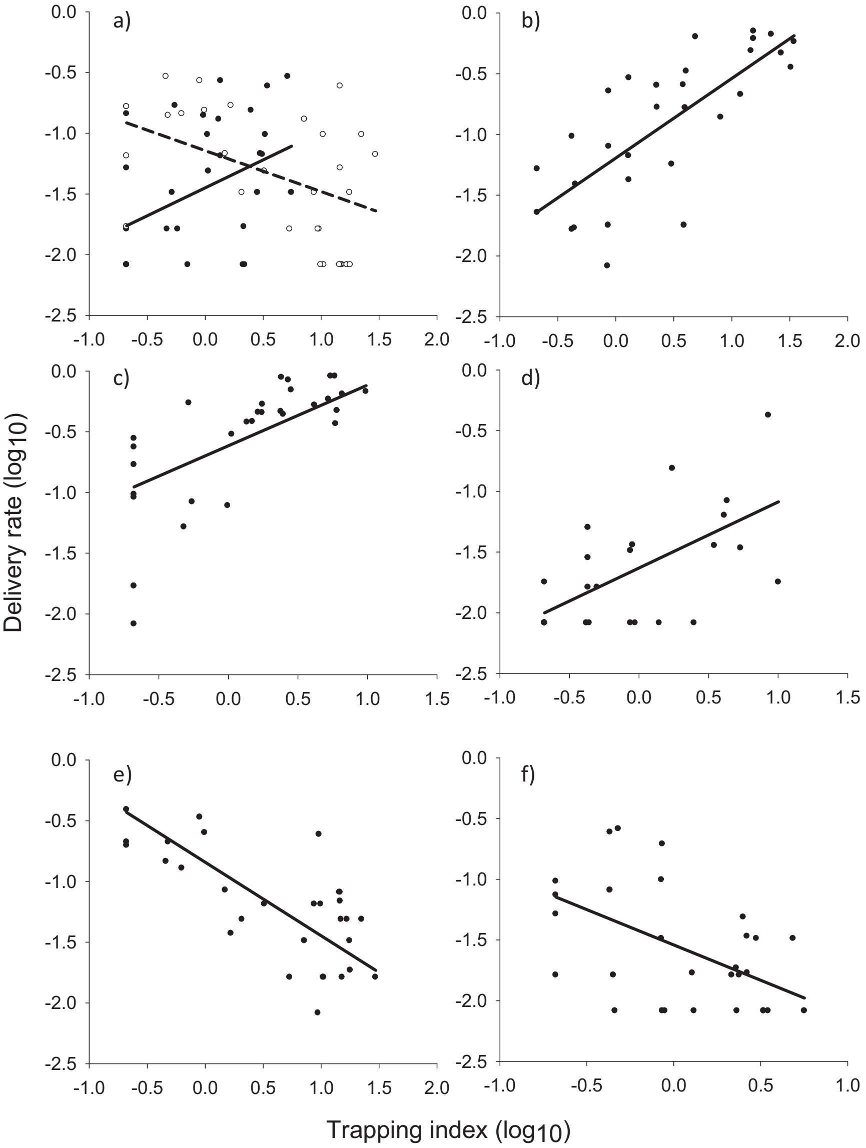

Figure 4. Effects of trapping indices of small mammals on prey item delivery rates at kestrel nests. a) The effect of the trapping indices of shrews (filled circles, solid line) and voles (open circles, dashed line) in open habitats on the delivery rate of shrews (at an average nestling age of 10.2 days). b) The effect of the trapping index of bank vole in all habitats on the delivery rate of bank vole. c) The effect of the trapping index of *Microtus* voles and grey-sided vole pooled in open habitats on the delivery rate of *Microtus* voles and grey-sided vole (at an average brood size of 4.5). d) The effect of the trapping index of wood lemming in all habitats on the delivery rate of wood lemming. e) The effect of the trapping index of voles (all species pooled) in open habitats on the delivery rate of avian prey (at an average brood size of 4.5). f) The effect of the trapping index of shrews in all habitats on the delivery rate of lizards (at an average daily mean temperature of 13.4 C^o).

Paper II

Functional response of kestrels to lizards determined by solar radiation and ambient temperature

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Abstract

Recent development in video monitoring has allowed collecting of data on prey deliveries at raptor nests, and this offers an opportunity to relate prey selection to short-term changes in environmental factors on a scale of hours. Whereas raptors may specialize on ectothermic prey at southern latitudes, only some generalist raptors may include such prey in their diet at northern latitudes. In particular, at northern latitudes the activity pattern of ectothermic reptiles is strongly dependent on the prevailing weather conditions. To test whether this dependence affects the exposure of reptiles to raptors, we used video recording of prey deliveries at nests of the Eurasian kestrel (*Falco tinnunculus*) at 61°N, where the common lizard (*Zootoca vivipara*) is the only lizard available to kestrels. The probability that a prey item delivered at a kestrel nest was a lizard, rather than another prey type, increased towards midday, and also increased independently with increasing ambient temperature, which on average was 20.2 ^{o}C when lizards were delivered compared to 15.7 ^{o}C when other types of prey were delivered. Thus, the kestrels´ capture of lizards in our study may be regarded as a functional response, where the abundance of lizards is determined by solar height and ambient temperature.

Keywords: common lizard, *Falco tinnunculus*, Eurasian kestrel, functional response, predation risk, solar radiation, temperature, thermoregulation, *Zootoca vivipara*

Introduction

How short-term changes in environmental conditions on the scale of hours affect prey selection by birds in general, and raptors in particular, is poorly known. Traditionally the diet of raptors has been estimated from prey remnants and regurgitated pellets collected at or near the nest during or after breeding, or from prey stored in the nest. This has restricted analyses of environmental effects to an inter-annual scale, as typical for studies of effects on diet of changes in prey abundance (e.g., Kellomäki 1977, Korpimäki 1988, Reif et al 2001, Millon et al. 2009). Collecting such data repeatedly during the breeding period has allowed relating diet change to environmental change on a shorter intra-annual scale, for instance during snow melt (e.g., Sonerud 1986). Further refinement in temporal resolution has traditionally required direct observations of prey deliveries from a blind near the nest, but this is very time consuming and has therefore rarely been used (e.g., Suomus 1952, Sulkava 1964, Stinson 1980, Newton 1986 and references therein, Redpath 1992). Moreover, the opportunity offered by such observations to relate prey type to environmental factors on a detailed temporal scale of hours has almost never been realised (for an exception see Stinson 1980). Recently, the development of various video techniques for recording prey deliveries at raptor nests (Steen 2009 and references therein) has allowed a cost-efficient collection of prey delivery data with temporally high resolution (e.g., Grønnesby and Nygård 2000, Selås et al. 2007, Tornberg and Reif 2007). Still, to the best of our knowledge, such data have hitherto not been used to relate changes in prey selection to corresponding short-term changes in environmental factors.

Raptors breeding at southern latitudes often prey upon ectothermic prey, and some to such an extent that they are classified as insect eaters or reptile eaters (Newton 1979). At northern latitudes, where reptiles and large insects are less abundant, generalist raptors may include such prey in their diet (e.g., Gil-Delgado et al. 1995, Selås 2001), but the mechanisms determining this inclusion is poorly known. Reptiles may minimize the risk of being preyed upon by staying hidden, but will face increased mortality when they have to leave the refuge for foraging or other activities (Lima and Dill 1990, Caro 2005). For ectothermic reptiles such as lizards external heat is required for maintaining an optimal body temperature to maximize physiological functions (cf. Avery 1987). Therefore, one purpose of leaving a refuge is to seek exposure to heat, either directly from solar radiation, or indirectly from warm air (Martin and Lopez 1999). Thermoregulatory behaviour utilized by lizards includes movement between sun and shade, or between hot and cold environments (Huey and Slatkin 1976 and references therein). An increased body temperature will increase sprint speed, foraging success and capacity to escape predation (Verwaijen et al. 2007 and references therein). In areas with a cool climate, the activities of lizards are therefore restricted to a certain period of the year, and certain hours of the day (e.g., Burke and Ner 2005).

The northernmost reptile, the common lizard (*Zootoca vivipara*), occurs over most of the Palearctic region northwards to the Arctic Sea, and inhabits open habitats such as peat bogs and heath lands (Grenot et al. 2000; Lorenzon et al. 1999; Pilorge 1987; Strijbosch 1988). Its activity pattern is strongly dependent on the prevailing weather conditions, and in particular the amount of solar radiation (Van Damme et al. 1987 and references therein). Furthermore, individuals from northern Sweden (67° N) were found to have higher endurance at lower temperature than individuals from southern Sweden (57° N; Uller and Olsson 2003). Common lizards respond to long-lasting cloudy weather by retreating underground, but resume activity quickly when direct sunlight is accessible (Van Damme et al. 1987). By being dependent on high ambient temperatures for their activity, and thus being more active on warmer days, lizards may suffer weather-dependent predation risk (Huey and Slatkin 1976). In particular, by basking, and especially by being more active after having obtained a higher body temperature, lizards are probably more visible to avian predators on sunny days and the warmest periods of the day. However, there is very limited data on how raptors respond to changes in prey availability associated with ambient temperature and time of day (see Stinson 1980 for an exception).

An important avian predator on the common lizard is the Eurasian kestrel (*Falco tinnunculus*)*,* hereafter called the kestrel, an open country raptor which takes mainly ground dwelling prey such as voles (Cricetidae), shrews (Soricidae), birds, lizards and insects (Village 1990). In this study we tested whether the kestrel more often prey upon common lizards at low temperatures, such as early in the morning or late in the evening, when the lizards can attain optimal body temperature only by basking in open habitats (cf. Van Damme et al. 1987 and references therein), or, alternatively, during spells of high temperatures and during mid-day periods when solar radiation is strongest, when the lizards are more active, shuttling between sun and shade, foraging and mating (Lorenzon et al. 1999).

Methods

Study area and video monitoring

The study was conducted in an area of c. 2000 km^2 in the boreal and hemi-boreal zones in Hedmark county in SE Norway (61^o N, 12^o E) during June and July in 2003 and 2005-2009. Here kestrel males providing for their family prefer to hunt in peat bogs with sparse trees (Løken 2009). This habitat is also favoured by the common lizard (Strijbosch 1988), which is the only lizard species occurring in the study area. The climate is relatively cool, so the lizards need to invest much time in thermoregulation for maintaining an optimal body temperature (cf. Herczeg et al. 2008). Average daily ambient temperature when recording prey deliveries was 15 C^o (range -1 to 31 C^o for the four daily records, see below). At summer solstice, sunrise and sunset is at 03:31 am and 10:55 pm local summer time (GMT + 2 hours), respectively, in the study area.

The frequency of lizards among prey captured by kestrels was estimated by video monitoring of prey deliveries to nest boxes used by kestrels for breeding. The nest boxes were mounted in solitary trees located in clear-cuts and heath bogs, surrounded by coniferous forest with only negligible patches of agricultural land. We had access to >100 kestrel nests each year, and mounted cameras in a total of 55 nests; nine in 2003, ten in 2005, six in 2006, ten in 2007, eleven in 2008, and nine in 2009. Each nest was filmed for two days in 2003, 2005 and 2006, for approximately 14 days in 2007, and for three days in 2008 and 2009. The filming days represent a wide range of brood ages from 8 to 29 days. Each filming day lasted c. 11 hours (c. 6 am to 5 pm) in 2003, c. 10 hours (6 am to 4 pm) in 2005, and c. 11 hours (c. 6-9 am to 6-9 pm) in 2006. In 2007-2009, the nests were filmed continuously throughout the whole day and night. For each nest, except the ones filmed in 2003, the original nest box was replaced with a new box designed to accommodate video monitoring. In 2003, a mini-dv camcorder was used for monitoring the kestrels. In 2005, an external camera was used in combination with a mini-dv camcorder as a recording unit. In 2006, both an external camera and a mini-dv camcorder were used in combination with a time lapse video recorder (VHS) and a hard disk recorder (HDD). In 2007-2009, we used a mini digital video recorder in combination with an external camera (for details, see Steen (2009)). Different set-ups between years were a consequence of technical improvement, i.e., more efficient installation procedure and easier maintenance. All set-ups were equally capable of recognizing prey items delivered at the nests.

Prey delivery and meteorological data

We identified each prey item delivered by the kestrels to type, i.e., whether it was a lizard, a shrew, a vole, or a bird, or, very rarely, a frog or an insect. In a few cases, the parent landed on the nest box with a prey item without providing it to the nestlings. Instead, the parent departed with the prey item, and later returned with the seemingly same prey item, which sometimes was more prepared (e.g., removed head, feathers or intestines). To avoid duplicate counting of prey items we counted only one delivery when the time between departure and return was 30 min or less in such cases (n=47). By using the probability of a prey delivered being a lizard as the response variable, and not the delivery rate of lizards per se, we were able to control for any diel pattern in the hunting activity of the kestrels. However, to control for the possibility that an increase in the probability of a prey item delivered being a lizard was caused by lizards being captured as an alternative when other prey types were less available, we also calculated separate time-specific delivery rates of lizards and other prey types.

The 55 nests monitored were in 47 different nest boxes; i.e., six nest boxes were filmed for two years and one for three years. Of the nest boxes filmed for two years, three were filmed in subsequent years, one was filmed three years apart, and two were filmed five years apart. The nest box filmed for three years was first filmed two years apart and then three years apart. In our study area, the kestrel is a migrant that arrives in April and May. Also in western Finland (63°N) the kestrel is a migrant, and only 25% of the males and 8% of the females reuse the same nest site in successive years (Tolonen and Korpimäki 1995). In Scotland (55°N), where the kestrel is partly resident, 29% of males and 18% of females reuse the same nest site in successive years (Village 1990). Applying these high turnover rates on our reuse of boxes for filming suggests that one individual or less of each sex would have been filmed at two nests. Thus, we assume that very few, if any, adult kestrel was involved in more than one of our 55 monitoring sessions. Therefore, we treated breeding pairs as the statistical unit.

To examine the effect of external heat on the probability that a lizard, rather than an item of another prey type, being captured by the kestrels, we used the ambient temperature at the time each prey item was delivered at the kestrel nests. The data on ambient temperatures were obtained from Trysil Vegstasjon official meteorological station, situated central in our study area (61°29' N, 12°27' E, at 360 m elevation), and on average 16.5 ± 1.0 km (range 3.1-28.8) from the nest boxes we filmed (n=47). Here, ambient temperature is recorded four times per day (01.00 am, 07.00 am, 01.00 pm and 07.00 pm local summer time (GMT + 2 hours)).

Based on these records, ambient temperature at the time of prey delivery was estimated by linear interpolation. To examine the effect of solar radiation on the probability that a lizard, rather than an item of another prey type being captured, we used a linear proxy for the solar height, namely the number of hours from solar midnight (01.13 am local summer time during our study) at the time each prey item was delivered at the kestrel nests, thus a variable taking any value between 0 and 12.

Statistical analyses

Statistical analyses were performed with the software R, version 2.8.1 (R Development Core Team 2008), using logistic multilevel regression. The response variable was whether a prey item delivered by the kestrel was a lizard or not (frequency). Explanatory variables were ambient temperature at the time the prey item was delivered, the number of hours from solar midnight, and the interaction term. The variables breeding pair and year were included as random effects (Pinheiro and Bates 2000) to control for any individual differences in the frequency of lizards among prey items delivered, for instance due to differences in prey abundance between territories or years. Different combinations of the variables in the global model were tested, where the model with the lowest AIC-value was selected. We kept to the most parsimonious model if the differences in ΔAIC were less than 2.0 after adding a variable (Burnham 2002). We used log-likelihood ratio tests to check for the significance of random effects. We compared the two fitted models with different specifications of the random effects and checked whether removal of a random effect caused a significant decrease in the log-likelihood ratio (Bolker et al. 2009). Breeding pair was kept as a random effect in the model regardless of its significance value to control for possible variation caused by individual differences. Year as a random effect was included in the final model only when being significant at α=0.10.

Figures were constructed by using Sigma-Plot version 9.01 graphic package (SPSS Inc.). Estimates are presented as mean ± SE.

Results

A total of 313 lizards were recorded delivered at the nests and provisioned to nestlings by the kestrels, constituting 5.7% of the total number of prey items recorded (n = 5499). The probability that a lizard, rather than an item of another prey type, was delivered increased significantly with increasing ambient temperature and with number of hours from solar midnight, with no interaction effect (Table 1, Fig.1). The random effect of 'year' did not contribute significantly to the model. However, 'breeding pair' had a significant random effect and was kept in the model (likelihood ratio test: $\chi^2 = 83.37$, *df* = 1, p < 0.001).

The lizards were delivered when ambient temperature on average was 20.2 ± 0.24 ^{o}C (n=313), compared to 15.7 ± 0.05 ^{o}C (n=5186) for the other prey types. The lowest ambient temperature when a lizard was recorded delivered was 7.1 ^{o}C and the highest 31.4 ^{o}C. The lizards were delivered between 06.42 am and 09.48 pm. Most of them were delivered between 10 am and 5 pm, when the average ambient temperature at the time of delivery ranged 19.1 - 22.0 ^{o}C (Fig. 2a). In comparison, prey items of other types were delivered between 02.48 am and 11.39 pm (Fig. 2b). The delivery rate of these other prey types did not vary between 7 am and 8 pm (Fig. 2b). Hence, the higher probability of a prey item delivered being a lizard at high ambient temperature and around midday was not an artefact of decreased availability and thus capture rate of other prey types under these conditions.

Discussion

The probability that a prey item being delivered at kestrel nests was a lizard independently increased with both increasing ambient temperature and proximity to midday compared to earlier and later in the day. While the delivery rate of prey items other than lizards was quite constant throughout the day, the delivery rate of lizards peaked around midday. This corresponds with the fact that ambient temperature on average was 20.2 °C and 15.7 °C, respectively, when lizards and prey items of other types were delivered. The lizards' activity level is known to vary with hydrological conditions and ambient temperatures (Lorenzon et al. 1999). Furthermore, the lizards' aerobic metabolic capacity, which alone is sufficient to supply the required energy for foraging, increases with increasing ambient temperatures in the range from 20 to 30 ^{o}C (Al - Sadoon 1987). Hence, lizards may spend more time foraging at high temperatures, and then be more vulnerable to predation by kestrels by being more detectable. Also, the activity pattern of the lizard is known to depend strongly on the prevailing weather conditions, in particular on solar radiation (Van Damme et al. 1987 and references therein).

Common lizards are smaller than the other prey types (except insects) taken by kestrels in our study area; estimated mean body mass of prey delivered at our kestrel nests were 5.3 g for lizards, 9.6 g for shrews, 20.3 g for voles, and 37.8 g for birds (Steen et al. 2010). The size distribution of prey items delivered at a raptor´s nest may be a biased estimate of the size distribution of prey items captured by the raptor, because allocation of prey for transport to the nest among those captured may not be random. In fact, raptors in general tend to carry larger prey to the nest and consume smaller at the capture site (the “load-size effect”; Sonerud 1992 and references therein). The kestrel in particular has been found to consume a higher proportion of common lizards at the capture site, compared to larger prey (Sonerud 1989). Thus, the proportion of lizards among prey items captured by the kestrels in our study was most likely higher than the proportion of lizards among prey items delivered. Moreover, according to the models presented by Sonerud (1992), the magnitude of this underestimation would depend on the proportion of lizards among prey items captured.

The kestrels´ capture rate of lizards in our study may be regarded as a functional response, where the availability of lizards is determined by solar height and ambient temperature (cf. Fig. 2a in Sonerud 1992, with lizards as the primary prey and the other and larger prey types as alternative prey). As long as this capture rate, as proportion of the total capture rate, is below a threshold, as at low solar radiation and low ambient temperature in our study, all lizards captured would be consumed at the capture site, and none would be delivered at the nest (cf. Fig. 2b in Sonerud 1992). Above this threshold, where more lizards are taken than is needed by the hunting kestrel to fulfil its own energy requirement, lizards would make up an increasing frequency of prey delivered. Thus, our estimate of the proportion of lizards among prey taken by kestrels, based on the sample of prey item delivered at the nest, would be less biased as the capture rate of lizards relative to other prey increases. If we had been able to record all prey items captured by our kestrels, and not only those delivered at the nest, we would have been able to estimate the real functional response curve for the kestrels´ predation on lizards. This curve would have laid above the recorded one for all values of ambient temperature and time from midnight, but most so for the lowest values and least for the highest. Factors other than the load-size effect may influence the allocation of captured prey for consumption at the capture site or transport to the nest, decreasing the difference between the real functional response curve and the one estimated from prey deliveries at the nest (Sonerud 1992, Korpimäki et al 1994). In any case, the biased estimate does not change our conclusion that the kestrels showed a functional response to lizards mediated by solar radiation and ambient temperature.

Our finding that lizards were more often captured by the kestrel as the ambient temperature increased is consistent with that of a study of predation behaviour in loggerhead shrikes (*Lanius ludovicianus*), where ambient temperature was assumed to be the main determinant of the attack rate on ectothermic prey through its effect on prey activity and thus exposure to predation (Craig 1978). Similarly, at one nest of the red-tailed hawk (*Buteo jamaicensis*), where most prey were ectothermic snakes, the probability that a prey item was delivered increased with increasing ambient temperature (Stinson 1980). Our finding of lizards becoming more often captured by the kestrel around midday independently of ambient temperature contradicts the prediction that thermal conditions make common lizards more vulnerable to predation by the kestrel early in the morning or late in the evening when it can attain optimal body temperature only by basking in open habitats (cf. Van Damme et al. 1987 and references therein). To the contrary, our findings support the prediction that common lizards would be most prone to predation during spells of high temperatures and at the time of day with the highest solar radiation near midday, when they are more active, shuttling between sun and shade (Lorenzon et al. 1999). However, since we did not collect data on the activity level of the lizards during our study, we are unable to distinguish whether the peak in lizard mortality through predation by kestrels at high solar radiation and ambient temperature is just due to a change in lizard activity rate, i.e., numbers of lizards active, or to changes in the vulnerability of lizards through changes in exposure and habitat use.

The probability that a prey item delivered at a kestrel nest was a lizard varied between breeding pairs. This may be due to differences in prey abundance and habitat composition between territories (cf. Costantini et al. 2005) or individual differences in prey selection behaviour. Some individuals may have been hunting in areas where lizards were absent or very few, or they may have specialized on certain prey types. Consistent individual differences, so called behavioural syndromes or animal personalities, have been documented in a variety of animals, including birds (Garamszegi et al. 2009; Kontiainen et al. 2009).

Given that the kestrels responded functionally to the availability of lizards as determined by solar height and ambient temperature, we would assume that during sunny and warm weather, the kestrels would switch foraging tactic to focus on lizards, or to restrict their search effort to microhabitats where lizards are most abundant (cf. Holling 1966). As a consequence of an increased presence of the kestrel, the lizards may need to increase their use of refuges and thus alter their thermoregulatory behaviour (cf. Martin and Lópes 1999). Hence, for the lizard, the benefit of obtaining optimal body temperature for maximizing physiological functions by exposure to external heat need to be traded against the increased risk of being preyed upon by the kestrel.

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Table 1. Parameter estimates from a logistic multilevel regression model with the frequency of lizards among prey delivered to kestrel nests as response variable, and ambient temperature (C^o) and hours from solar midnight (01.13 am local summer time) as explanatory variables (n = 5499). The estimates are corrected for the random effect of breeding pair identity (n = 55).

Explanatory variable	Estimate	SE±	z	p
(Intercept)	-7.72	0.46	-16.61	<0.001
Ambient temperature	0.18	0.02	8.71	<0.001
Hours from solar midnight	0.19	0.03	5.72	<0.001

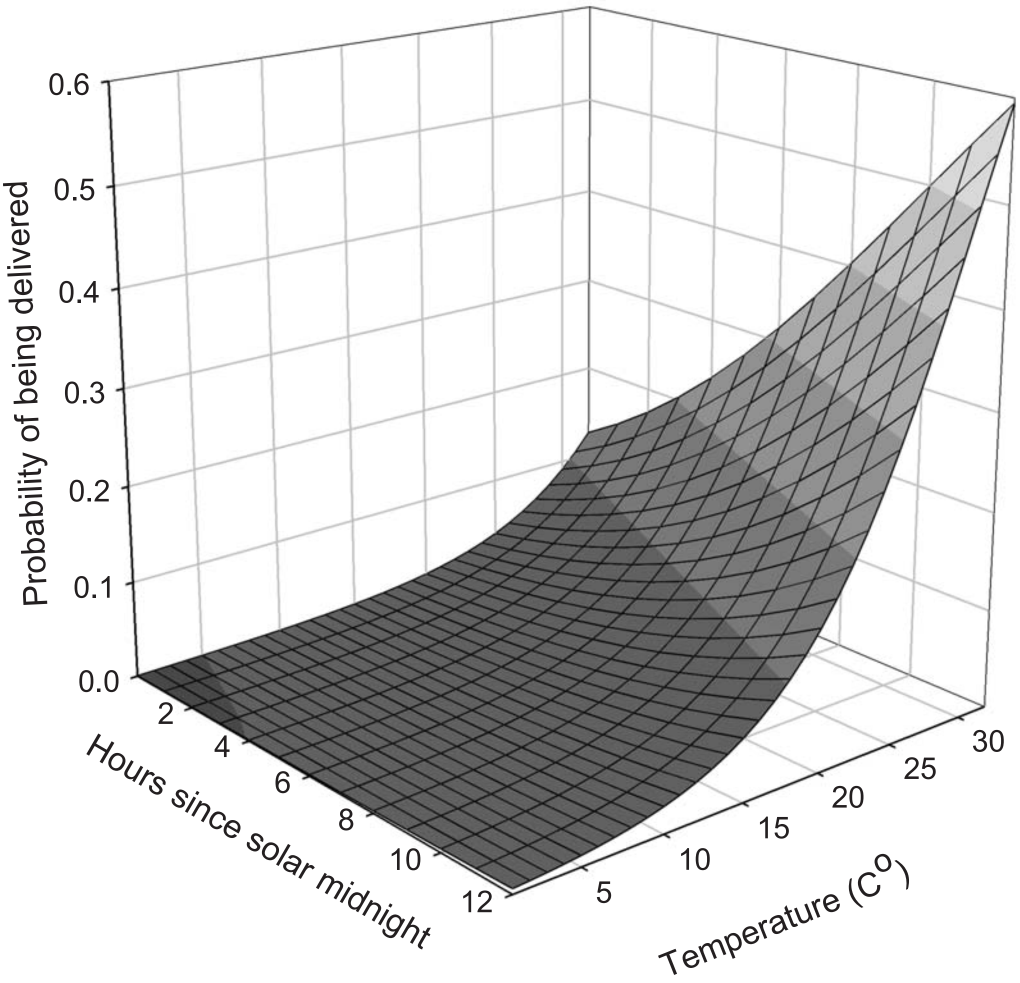

Figure 1. The probability of a lizard rather than an item of another prey type being delivered at kestrel nests as a function of ambient temperature and hours from solar midnight, with the plane describing the complete logistic regression model (calculated from the parameter estimates). Note that the scale on the axis denoting hours from solar midnight (01.13 am local summer time) is an approximate measure of solar radiation.

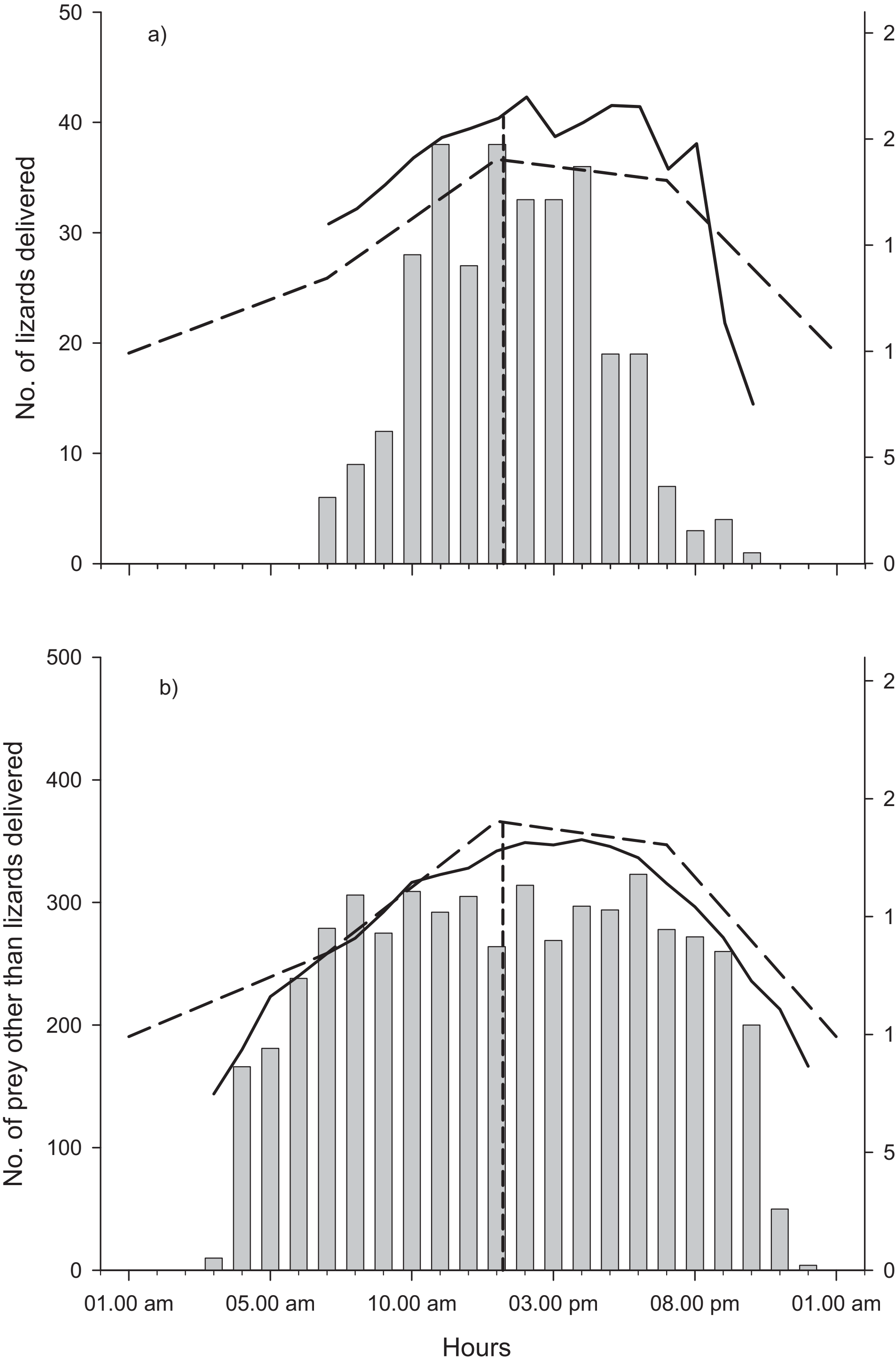

Figure 2. Number of prey items delivered at kestrel nests during each hour of the day (bars), average ambient temperature at the time of prey delivery (solid curve), average ambient temperature each hour of the day during the study period (dashed curve), and horizontal dashed line stating the midday (01.13 pm). a) Lizards (n=313). b) Other prey types (insects, amphibians, mammals and birds; n=5186).

Paper III

Do females really capture larger prey than males in breeding raptors? Size-dependent prey-allocation by male Eurasian kestrels *Falco tinnunculus*

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Abstract

Among the many hypotheses attempting to explain why females are larger than males in most raptors in contrast to most other birds, those sharing the theory that inter-sexual food competition would select for segregation in prey size predict that females take larger prey than males. In most raptors there is a marked separation of breeding duties between the sexes, with the female performing most or all incubation, brooding and feeding of nestlings, while the male provides most or all food for the family, assisted by the female in the later part of the nestling period, if at all. Most raptors take relatively large prey, which may be impossible for nestlings to handle and thus require extended parental assistance for partitioning and feeding. Whereas even young nestlings may consume smaller prey unassisted, the female have to dismember larger items until the nestlings become older. By video recording prey delivered at nests of the Eurasian kestrel *Falco tinnunculus* and simultaneously observing prey transfer from male to female away from the nest, we found that the male selectively allocated smaller items, in particular common lizards *Zootoca vivipara* and shrews (*Sorex* spp.) directly to the nestlings, whereas larger items, in particular avian prey, were delivered to the female for further processing before the final transport to the nest and feeding of nestlings. Hence, based solely on the video recordings from the nests females appeared to have taken larger prey than males, while in reality there was no size difference between items captured by males and females. If such size-dependent prey allocation is general in raptors where the female retrieve prey from the male outside the nest, any inter-sexual difference in prey size previously found by recording prey deliveries at the nest must be re-evaluated. Failure to find any feeding niche separation between the sexes during breeding would exclude a proposed mechanism for the evolution of RSD in raptors.

Keywords: Eurasian kestrel, *Falco tinnunculus*, foraging, prey handling, prey selection, raptor, RSD, sex roles

Introduction

In most raptors, i.e. hawks (Accipitriformes), falcons (Falconiformes) and owls (Strigiformes), females are larger than males, in contrast to most other birds (Newton 1979, Andersson 1994). Among the many hypotheses proposed to explain this reversed sexual size dimorphism (RSD), for which there is no consensus (e.g. Mueller 1990, Andersson 1994, Massemin et al. 2000, Krüger 2005), some focus on inter-sexual food competition and share the assumption that inter-sexual differences in prey selection would enable the pair to exploit a wider range of prey resources and thereby minimizing competition between the mates (e.g. Selander 1966, Snyder & Wiley 1976, Newton 1979, Andersson & Norberg 1981, Temeles 1985). These niche differentiation hypotheses predict females to take larger prey than males, particularly in raptors specializing on avian prey, which show a higher degree of RSD than other raptors (Newton 1979). Avian prey may be less abundant than other prey types and are also more difficult to capture (Andersson & Norberg 1981, Temeles 1985).

In most raptors there is a marked separation of duties between the sexes during breeding, with the female performing most or all incubation, brooding and feeding of nestling, while the male provides most or all food for the family, assisted by the female in the later part of the nestling period, if at all (e.g. Newton 1979, 1986, Cramp & Simmons 1980, Cramp 1985, Wiehn & Korpimäki 1997, Eldegard et al. 2003, Sunde et al. 2003, Eldegard & Sonerud 2010). Most raptors take large prey for their size, which may be impossible for nestlings to handle, requiring extended parental assistance for partitioning and feeding (Newton 1979, 1986, Cramp and Simmons 1980, Cramp 1985). The morsels fed to nestlings are surprisingly small, e.g. 0.3 g for the sparrowhawk *Accipiter nisus* (Andersen 2003), 0.6 g for the Eurasian kestrel *Falco tinnunculus* (Fargallo *et al*. 2003), 1.1 g for the osprey *Pandion haliaetus* (Poole 1985) and 1.7 g for the common buzzard *Buteo buteo* (Aanonsen 2003). Therefore, raptors may need a long time to feed their nestlings from a prey item; sparrowhawks spend up to 45 min feeding their nestlings about 500 morsels from one prey (Newton 1986, Andersen 2003). The duty of dismembering prey and feeding the morsels to the nestlings falls on the female, who would stay at the nest or close by, retrieving the items captured by the providing male (e.g. Newton 1979, 1986), and thus relieving him from feeding and allowing him to resume hunting sooner (Slagsvold & Sonerud 2007).

Prey items taken by raptors vary greatly with respect to the efficiency with which the nestlings can ingest them unassisted (Steen et al. 2010a). Raptor nestlings become sooner able to ingest cylindrical prey with small appendages, such as lizards and shrews, than prey with protruding appendices that in addition need to be plucked, such as birds, and sooner able to ingest smaller items than larger ones of the same type (Sonerud et al. 2010, Steen et al. 2010a). Thus, at any stage of the nestling period, the need for maternal assistance would vary with prey type and prey size (Sonerud et al. 2010). Among the prey that the male carries back to the nest, therefore, those that the nestlings are able to ingest unassisted may be delivered directly to the nestlings, whereas those that require parental assistance need to be delivered to the female for further processing and feeding (Slagsvold & Sonerud 2007, Sonerud et al. 2010).

Studies of sex-specific prey selection in raptors have relied on observations of prey items delivered at the nest and identification of the sex delivering the item, traditionally by a hidden observer, and more recently by use of a video camera (e.g. Redpath et al. 2001, Lewis et al. 2004, Tornberg & Reif 2007). This relies on the assumption that the sex delivering a prey item at the nest has captured this prey. However, in raptors prey transfer from male to female usually takes place away from the nest (e.g. Newton 1986, Village 1990, Kenward 2006), outside the view of the observer, or the video camera. If the male´s allocation of a prey item directly to the nestlings or indirectly via the female is independent of prey type and prey size, an estimate of the intersexual difference in prey selection based on deliveries at the nest would be correct. However, if his prey allocation depends on prey type or prey size, any estimate of an intersexual difference in prey selection would be biased. Because items inefficient for the nestlings to ingest unassisted, such as larger prey, are more likely to be transferred to the female, we predict that observation of prey deliveries at raptor nest would overestimate any inter-sexual difference in prey size selection. Thus, the larger sex would appear to have captured the larger prey.

Here we use data on prey deliveries in the Eurasian kestrel to demonstrate non-random allocation of prey items from the providing male directly to the nestlings or indirectly via the female for further processing, resulting in an apparent intersexual difference in prey selection in spite of there being none, with the female apparently selecting larger prey than the male. The Eurasian kestrel, hereafter termed the kestrel, is a relatively small falcon (male body mass c. 200 g) with a moderate RSD; females have on average c. 4% longer wing cord than males (Village 1990). The kestrel is particularly well suited for a study of the allocation of prey from the male to offspring and mate, because its diet includes insects, reptiles, mammals and birds

(Village 1990), and thus prey types with a large variation in body mass and ingestion time (Steen et al. 2010a). Also, identifying the sexes and recording their prey allocation behaviour is facilitated because kestrels are sexually dichromatic and live in open habitats (Village 1990). Finally, kestrels readily use open nest boxes and are tolerant to disturbance, which facilitates recording of prey deliveries and prey ingestion.

We recorded allocation of prey in kestrels provisioning for their nestlings, by simultaneously watching the kestrels´ behaviour outside the nest, and by filming their behaviour in the nest. Our questions were: i) Do prey items captured by male and female differ with respect to size, i. e. type and body mass? ii) When the male returns with a prey item, will prey size influence whether he delivers the item directly to the nestlings or to the female who then dismembers and feeds it to the nestlings? iii) Do prey items delivered at the nest by male and female, as would be recorded by video, differ with respect to size? We will discuss the implications of the answers to these questions for the existence of intersexual difference in prey selection and the evolution of RSD in raptors.

Methods

Study area and species

The study was conducted in June-July in 2003 and 2005 within a c. 1000 km^2 area (61°07´-61°31´ N; 12°00´- 12°43´ E) in the boreal and hemi-boreal zones in Trysil municipality, Hedmark county, south-eastern Norway. Here >100 pairs of the kestrel breed in nest boxes each year, of which we filmed nine in 2003 and ten in 2005. The average (± SE) distance to the nearest other monitored nest was 6.7 ± 3.7 (range 2.1-35.8) km in 2003 and 3.1 ± 0.6 (range 0.6-7.4) km in 2005. All nests were in boxes with open front, put up 5-15 m above ground in trees located in bogs, clear-cuts or open forest at altitudes of 300-700 m. The study area is covered by coniferous forest intensively managed by modern forestry techniques, i.e. harvesting by unselective clear-cutting, regeneration by planting, and thinning by selective cutting. The proportion of bogs is relatively high, whereas there is only a negligible area of agricultural land in scattered patches.

In our study area, the kestrel is a migrant that arrives in April and May. Also in western Finland (63°N) the kestrel is a migrant, and only 25% of the males and 8% of the females reuse the same nest site in successive years (Tolonen & Korpimäki 1995). In Scotland (55°N), where the kestrel is partly resident, 29% of males and 18% of females reuse the same nest site in successive years (Village, 1990). Thus, although we filmed one nest box both in 2003 and 2005, most likely different individuals were involved. Therefore, when treating breeding pairs as the statistical unit, we regarded 19 as the sample size.

Recording behaviour in the nest

Each brood was filmed for two days, except one in 2003, which was filmed for one day only. In 2003, the first filming were done when brood age (i.e. the age of the last hatched nestling) was 12.3±0.7 days (range 8-15), and the second when brood age was 25.9±0.6 days (range 23-28). In 2005, each brood was filmed on subsequent days with one exception, first when brood age was 12.6±0.8 days (range 8-16), and second when brood age was 13.8±0.8 days (range 9-17). Brood size was 5.0±0.3 (range 4-7) on both film days in 2003, and 3.1±0.5 (range 1-5) in 2005. None of the broods were abandoned during the study.

In 2003, food provisioning in the nest was recorded with a digital camcorder, Canon MV550i, with a WD-30.5 wide-angle lens. The camcorder was mounted on the top of the nest box with the lens pointed through the roof and towards the open front of the box, so that the prey was in view from arriving with the adult kestrel until being consumed by the nestlings. To habituate the kestrels to filming a dummy camcorder was mounted in the same position 1-2 days before filming. JVC Mini DV 80ME cassettes, which lasted 2 h 40 min (2 x 80 min) in long play mode, were used. Power supply to the camcorder was provided by a standard Canon battery pack BP-535 (7.4V, 3500mAh). To switch cassettes, the nest tree had to be entered, and thus any ongoing feeding session was interrupted. Each brood was video-recorded for an average of 10 h 40 min (4 cassettes) between 6 AM and 5 PM each day.

In 2005, each of the ten original nest boxes was replaced with nest box of plywood special-made for filming (36 cm x 28 cm x 31 cm) 2-4 days prior to filming, allowing the kestrels to habituate. A special made camera-top made of plywood to fit the nest boxes was used at all nests, and was relocated one day prior to filming. This top contained a wired 18LED night vision CCTV camera lens, size 50 mm x 45 mm x 45 mm, waterproof for outdoor use. The lens was positioned in such an angle so that the prey was in view from arriving with the adult kestrel until being consumed by the nestlings. Power supply to the lens was provided by a 12 V lead battery (10 Ah) placed on the ground at the base of the nest tree. A connection made of 50 m of modified RCA video cables between the lens and a Canon MV850i digital camcorder allowed monitoring and recording prey deliveries and handling from a hide on the ground (see below). In this way cassettes could be switched in the hide without disturbing the kestrels. Power supply to the camcorder was obtained from a 12 V lead battery (10 Ah) with a voltage converter (from 12 to 8.4 V). Panasonic Mini DV 80 L-PLUS cassettes were used, which lasted 2 h in long play mode. Each brood was filmed for an average of 10 h (5 cassettes) from 06.00 AM to 04.00 PM each day.

Different set-ups between years were a consequence of technical improvement, and both set-ups were equally capable of recognizing prey items delivered at the nests.

Recording behaviour outside the nest

On each filming day the kestrels´ allocation of each prey item prior to delivery at the nest was recorded by observations from a hide on the ground simultaneous with the video recording. In 2003, the hide was placed 30-100 m from the nest tree, depending on the local topography. In 2005, the 50 m video cable from the nest box to the camcorder (see above) restricted the distance between the nest tree and the hide to 25-35 m. The observations from the hide and the video recordings each covered c 192 hours in 2003 and c 200 h in 2005.

For each prey item delivered at the nest, time, type of prey (insect, common lizard *Zootoca vivipara*, shrew (*Sorex* spp.), vole (Microtinae) or bird), and the sex having captured the item and the sex delivering it was scored. By synchronizing the observers´ watches with the time recorder in the camcorder, observed as well as suspected deliveries could be verified when later watching the video (see below). The male was defined to have captured the prey if one of the following three conditions was fulfilled: i) The male was observed to deliver the prey at the nest (females never deliver prey to males). ii) The male had been observed to deliver the prey to the female outside the nest. iii) The female had been recorded to arrive with a prey item at the nest without the male being observed, but his calling had been heard prior to the delivery. The female was defined to have captured the prey if she had been recorded to arrive with a prey item at the nest without the male being observed or his calling being heard prior to the delivery. Prey deliveries from male to female mostly happen near the nest, often repeatedly at the same site (Village 1990). Because the male usually vocalise in a special way prior to delivery (Village 1990), and because of the open landscape around the nest boxes, prey deliveries were fairly easy to record from the hide, unless there was strong wind making the male´s calling difficult to hear. In a few cases the female retrieved cached prey items, and for these the sex having captured the item could not be scored.

Video analysis

The video recordings were analyzed on a monitor. For each prey delivery and subsequent feeding session the prey item was identified (see below) and the sex of the delivering parent was determined. The handling time of a prey item (measured to the nearest second) was defined to include preparation (e.g. plucking) by the female or by the nestlings, the female partitioning of food to the nestlings, the nestlings feeding unassisted, and the female post-feed cleaning, but not the nestlings post-feed cleaning. If an item was consumed in two bouts, the handling time of the first and the second were pooled. Female partitioning time for each prey item was defined as the time elapsed from the moment she bent her head down to tear off the first piece until the item had been completely consumed or abandoned. In some cases the female self-fed for a short time, and this is included in female partitioning time. If the nestlings fed unassisted, they would either monopolize the prey item or share it with one or more siblings (Steen et al. 2010a). In the first case, feeding time was taken as the time that one nestling spent on self-feeding, from the moment it lowered its head to tear off the first piece until the item was completely consumed or abandoned, or, if the prey item was swallowed whole, the time elapsed from the moment the nestling received the item from the parent until its swallowing movements ended. In the second case, feeding time was taken as the time elapsed from the moment the nestlings grabbed the prey until the prey were totally consumed or abandoned. Sibling fights over food possible to separate from feeding were excluded from feeding time. In a few cases the female partitioned part of an item and the nestlings later self-fed on the same item. In those cases, female feeding time and nestling feeding time were separated, but the two bouts were added in total feeding time and classified as assisted feeding. If the female or nestlings stopped feeding for longer than 4-5 s, the pause was excluded from the feeding time. For some prey items delivered handling time could not obtained, either because the handling was difficult to view, the item was not completely eaten, or the feeding was interrupted by prey delivery or tape change.

Almost all vertebrate prey items were identified to species, while insect prey were identified to order. Body mass of lizards and small mammals has a relatively high intra-specific variation, and was therefore estimated from their size on the video frame, as described in detail by Steen (2004, 2010) and Løw (2006). Because this required the whole body to be exposed, the body mass of some lizards and mammals could not be estimated. Body mass of birds has a relatively small intra-specific variation, and was therefore obtained from Selås (2001) and from the data most pertinent to Fennoscandia and the breeding season in Cramp & Simmons (1983), Cramp (1985, 1988, 1992) and Cramp & Perrins (1993, 1994a,b). For passerines, juveniles were assigned the same body mass as adults, whereas for grouse and shorebirds, the body mass of juveniles was estimated from appearance and relative size on the video frame. Two avian prey were passerine nestlings impossible to identify to species, so their body mass could not be estimated. The estimated body mass of avian prey delivered at the nests is listed in Steen (2004) and Løw (2006).

A few shrews, and many voles, were decapitated prior to delivery at the nest (Steen et al. 2010b). The head of a vole was estimated to weigh 16.5% of the total body mass (Asakskogen, 2003). Because the body mass of decapitated shrews and voles had been estimated from their size on the video frame on delivery, we divided the estimated body mass of decapitated shrews and voles with 0.835 to attain the body mass prior to decapitation.

Statistical analyses

Statistical analyses were performed with the software R, version 2.8.1 (R Development Core Team 2008), using the generalized linear mixed effect model by the Laplace approximation in the lme4 package (Pinheiro & Bates 2000). Each prey item was the population unit in statistical tests. We first tested whether prey size affected the probability that a prey item delivered had been captured by the male, then whether prey size affected the probability that the male delivered a prey item he had captured directly to the nestlings rather than to the female, and finally whether prey size affected the probability that an item was delivered at the nest by the male. As a measure of prey size we used both prey type (lizard, shrew, vole or bird) and prey body mass as explanatory variables. Nest ID and year were included as random factors, the former to control for a possible variation caused by individual differences in prey capture and allocation, and the latter to control for potential inter-annual variations in conditions that may influence any inter-sexual difference in prey capture and allocation.

We used log-likelihood ratio tests to check for the significance of random effects. We compared the two fitted models with different specifications of the random effects and checked whether removal of a random effect caused a significant decrease in the log-likelihood ratio (Bolker et al. 2009). Breeding pair was kept as a random effect in the model regardless of its significance value to control for possible variation caused by individual differences. Year as a random effect was included in the final model only when being significant at α=0.10.Figures were constructed by using Sigma-Plot version 9.01 graphic package (SPSS Inc.). Estimates are presented as mean ± SE.

Results

Of the 367 prey items that were recorded delivered to the 19 kestrel nests, 1 was a frog, 9 were insects, 66 common lizards, 76 shrews, 79 voles, and 129 birds, whereas 5 were unidentified mammals and 2 were prey remains. The frog, the unidentified mammals and the prey remains were excluded from the analysis. Females captured all the insects, while both sexes captured lizards, shrews, voles and birds. The insects were therefore excluded in the further analysis.

The male had captured 69% of the 341 vertebrate prey items for which the capturing sex was determined. In a univariate nominal logistic regression model there was a significant effect of prey type on the probability that an item had been captured by the male (likelihood ratio test; χ^2=8.43, d.f.=3, p=0.038). Lizards, shrews, voles and birds made up 18%, 20%, 22% and 41%, respectively, of the 234 items that the male had captured, compared to 23%, 26%, 25%% and 25 % of the 107 items that the female had captured. Birds were significantly more likely to have been captured by the male than were lizards, shrews and voles, However, when nest ID was included as a random factor in a generalized linear mixed effect model the effect of prey type on the probability that an item had been captured by the male became non-significant, whereas the effect of nest ID was highly significant. Year did not contribute to the model. The probability of being captured by the male did not differ significantly between any of the four prey types (Table 1a, Fig. 1a).

Among the 233 prey items that the male had captured and delivered (one vole was captured, but not delivered), 24% were delivered directly to the nestlings. The probability that the male delivered an item directly to the nestlings rather than to the female was significantly affected by prey type, both in a univariate model (likelihood ratio test; χ^2=30.84, d.f.=3, p<0.0001) and in a generalized linear mixed effect model with nest ID as a random factor (Table 1b). Year did not contribute to the model. The male delivered 54% of the lizards he had captured directly to the young, compared to only 28% of the shrews, 22% of the voles and 9% of the birds. Among the items captured by the male, lizards were significantly more likely to be delivered directly to the nestlings than were shrews, voles and birds, and shrews and voles were significantly more likely to be delivered directly to the nestlings than were birds, while the probability of being delivered directly to the nestlings did not differ significantly between shrews and voles (Table 1b, Fig. 1b). Estimated body mass of vertebrate prey delivered at the kestrel nests was 5.4 ± 0.3 g (n=53) for lizards, 9.6 ± 0.3 g (n=64) for shrews, 20.4 ± 1.4 g (n=50) for voles and 38.1 ± 2.6 g (n=116) for birds. Estimated handling time in the nest for prey items consumed by the nestlings unassisted was 39.9 ± 7.9 s (n=45) for lizards, 151.3 ± 16.3 s (n=36) for shrews, 280.6 ± 51.0 s (n=22) for voles, and 624.6 ± 90.2 s (n=14) for birds. Thus, the male allocated larger prey, which took longer to consume for the nestlings, more often to the female.

As a consequence of the male´s selective allocation of small prey types directly to the nestlings and large prey types to the female, there was a significant effect of prey type on the probability that an item was delivered to the nestlings by the male as recorded solely by video (likelihood ratio test; χ^2=21.77, d.f.=3, p<0.0001), even when nest ID was included as a random factor (Table 1c). Year did not contribute to the model. Lizards, shrews, voles and birds made up 40%, 24%, 20% and 16%, respectively, of the 55 items that the male delivered to the nestlings, compared to 15%, 21%, 23%% and 41 % of the 294 items that the female delivered. Lizards were significantly more likely to be delivered by the male than were shrews, voles and birds, and shrews were significantly more likely to be delivered by the male than were birds, while the probability of being delivered by the male did not differ significantly between shrews and voles, or between voles and birds (Table 1c, Fig. 1c).

The estimated body mass of a prey item delivered did not significantly affect the probability that it had been captured by the male (likelihood ratio test; χ^2=0.03, d.f.=1, p=0.87), and was on average 21.4 ± 1.6 g (n=194) for those captured by males and 21.9 ± 2.4 g (n=83) for those captured by females. This was also the case when including nest ID as random factor (Fig. 2a). Nest ID had a significant effect (likelihood ratio test; χ^2=7.10, d.f.=1, p = 0.008), while year did not contribute to the model.

The estimated body mass of a prey item captured by the male significantly affected the probability that he delivered the item directly to the nestlings rather than to the female (likelihood ratio test; χ^2=5.86, d.f.=1, p=0.016), and was on average 15.5 ± 3.0 g (n=46) for those he delivered directly to the nestlings and 23.2 ± 1.7 g (n=148) for those he delivered to the female. When including nest ID as random factor the effect of the estimated body mass on the probability that the male delivered the prey item directly to the nestlings became only nearly significant (p=0.069, Fig. 2b). Nest ID had a highly significant effect (likelihood ratio test: χ^2=11.52, d.f.=1, p <0.001*)*, while year did not contribute to the model.

Again, as a consequence of the male´s selective allocation of smaller prey items directly to the nestlings and larger ones to the female, the estimated body mass of a prey item significantly affected the probability that the item was delivered at the nest by the male as recorded solely by video (likelihood ratio test: χ^2=6.45, d.f.=1, p=0.011), and was 15.5 ± 3.0 g (n=46) for those delivered by males and 23.8 ± 1.5 g (n=237) for those delivered by females. When including nest ID as random factor the effect of the estimated body mass on the probability that a prey item was delivered by the male became only nearly significant (p=0.053, Fig. 2c). Nest ID had a highly significant effect (likelihood ratio test: χ^2=9.89, d.f.=1, p =0.002*)*, while year did not contribute to the model.

Discussion

Apparently avian prey were more likely than other prey types to have been captured by the male, but this effect disappeared when we corrected for nest ID. The estimated body mass of a prey item did not affect the probability that the male had captured the item. Thus, we were unable to find any difference in size between prey captured by male and female kestrels. However, the size of a prey captured by the male affected the probability of the prey being delivered directly to the nestlings rather than to the female. Smaller prey items, in particular lizards, were more likely to be delivered directly to the nestlings, whereas larger items, in particular birds, were more likely to be delivered to the female for further processing before being fed to the nestlings. In consequence, and as would have been recorded by solely filming prey deliveries at the nest, smaller prey items, in particular lizards, but also shrews, were more likely to be delivered on the nest by the male, whereas larger prey items, in particular birds, were more likely to be delivered on the nest by the female. Lizards in particular are small prey, with an average estimated body mass of 5 g in our study, and kestrel nestlings readily become able to ingest them unassisted (Sonerud et al. 2010, Steen et al. 2010a). Shrews are larger, with an average estimated body mass of 10 g in our study, but kestrel nestlings soon become able to ingest these unassisted as well (Steen et al. 2010a). Voles, on the other hand, and in particular birds, are large prey, with an average estimated body mass of 20 g and 38 g, respectively, in our study, and are difficult to ingest unassisted until the nestlings are older (Sonerud et al. 2010). This is reflected in the fact that average ingestion time of nestlings feeding unassisted was 40 s, 151 s, 281 s and 625 s when the prey item was a lizard, a shrew, a vole and a bird, respectively. In addition, the parents decapitate larger voles and birds prior to feeding them to the nestlings (Steen et al. 2010a), and birds are also plucked prior to delivery at the nest (Steen 2004, Løw 2006). Note that in the present study only the female captured the insects delivered to the nestlings, so we excluded insects from the analysis. This make the tests conservative, because including insects would reduce the mean prey size for females relative to males. In later video filming at kestrel nests we have also recorded males feeding nestlings directly with insects (R. Steen et al. unpublished data).

Our findings suggest that there are at least two pitfalls in analyzing data on inter-sexual differences in the diet of raptors. Firstly, the availability of prey may have differed between the individual birds studied (cf. McDonald et al. 2003). Thus, care must be taken to avoid comparing data for males and females hunting in different areas or at different times (Village 1990). The most correct comparison would be of mates hunting in the same area simultaneously, i.e. either mates delivering prey to offspring (this study), or mates residing in the same territory outside the breeding season (Sunde et al. 2003). If prey items are used as population unit, pair identity must be corrected for (Sunde et al. 2003, cf. Korpimäki et al. 1994). Our data did indeed show that if we did not correct for nest identity avian prey were more likely to have been captured by the male compared to other prey types, illustrating the pitfall of pooling all data from each sex in a population. We found significant effects of nest identity in all the tests we performed, in particular for the allocation of prey items directly to nestlings or indirectly via the female for processing, so any inter-sexual difference in behaviour related to prey selection may appear larger than it really is if not corrected for nest identity. For instance, in the sparrowhawk Newton (1986) found that females on average delivered larger prey than males. However, larger prey were more often delivered at nests in poor habitat than at nests in rich habitat (Newton 1986), and females assisted the male in hunting more in pairs nesting in poor habitats than in pairs nesting in rich habitat (Newton 1986). Thus, larger prey associated with female delivery in the sparrowhawk may be an artefact of not correcting for nest identity. Therefore, larger average size of prey delivered by females than of prey delivered by males in studies where data from several nests were pooled, such as for gyrfalcons (*Falco rusticolus*), sharp-shinned hawk *Accipiter striatus* and Cooper´s hawk *Accipiter cooperi* (Snyder and Wiley 1976, Poole and Boag 1988), cannot be taken as evidence for females selecting larger prey than males. In fact, the few studies that has corrected for nest identity, viz. prey delivered at nests by Cooper´s hawk (Kennedy and Johnson 1986) and goshawk *Accipiter gentilis* (Boal and Mannan 1996, Grønnesby and Nygård 2000), and prey remnants in pellets of radio-tagged tawny owls *Strix aluco* (Sunde et al. 2003), failed to find a difference in prey size between the sexes.

Secondly, previous studies on inter-sexual differences in prey selection by raptors have been based on assigning parent sex to prey deliveries at the nest. If we had limited our data to prey observed being delivered at the nest, i.e. our video recording, the analysis would have shown that kestrel males took smaller prey than their mates, even if we corrected for nest identity. The reason for this bias is that the male allocated prey between his nestlings and his mate differentially depending on type; he delivered 46% of the lizards, 71% of the shrews, 78% of the voles and 91% of the birds that he had captured to the female, who then brought them to the nest. Thus, if we had used our data on what the kestrels delivered at the nest as a basis for our estimate of what the kestrels had captured, we would have erroneously concluded that the mates took different-sized prey, with the male taking a higher proportion of the smaller lizards and the female a higher proportion of the larger birds. Thus, in raptors where prey captured by the male may be transferred to the nestlings via the female outside the nest, size-dependent allocation of prey items as observed in our study, with the male delivering smaller prey directly to the nestlings, and larger to the female for partitioning, would result in an overestimation of any inter-sexual difference in prey captured. For instance, at each of three sparrowhawk nests observed at close range from a blind by Geer (1981), the female arrived with larger items than the male, but because the female had retrieved some of these prey from the male, the observed inter-sexual difference may have been due to selective allocation of smaller prey to the nestlings and larger items to the female. In fact, in two of the three studies of *Accipiter* hawks that failed to find an inter-sexual difference in prey size (Kennedy & Johnson 1986, Boal & Mannan 1996), prey were assigned to male and female in a similar way as in our study. Thus, inter-sexual differences in prey selection by raptors cannot be estimated only by recording prey deliveries at the nest, unless the male always delivers the prey items he has captured directly at the nest. Such direct deliveries occur only in a minority of raptors, e.g. in the Tengmalm´s owl *Aegolius funereus* (Cramp & Simmons 1980, Cramp 1985). Unfortunately, prey transfer from male to female may be difficult to observe, either because of restricted visibility in the nest surroundings, such as for forest dwelling raptors, e.g. sharp-shinned hawk, Cooper´s hawk, sparrowhawk and goshawk, or because prey transfer may take place very far from the nest, e.g. gyrfalcon (Poole and Boag 1988, Kenward 2006).

We were unable to find any difference in size between vertebrate prey captured by male and female kestrels. Average estimated body mass of prey captured was 22 g, which amounts to c. 10% of the body mass of kestrels. If ingestion rate is higher for smaller prey items than for larger ones, as is the case when adult raptors are self-feeding and nestling raptors are feeding unassisted (Slagsvold & Sonerud 2007, Slagsvold et al. 2010, Steen et al. 2010a), both sexes should take small prey as long as these are abundant, and switch to larger prey only when smaller become less abundant (Slagsvold and Sonerud 2007). Because females are larger than males, the upper size limit for prey possible to subdue will be larger in females than males, and relatively larger with increasing RSD. We would therefore expect a difference in prey size between sexes when small prey are scarce, and most so in species with large RSD. Thus, the most likely candidates for females capturing larger prey than males would be sparrowhawks and goshawks nesting in poorer territories, or wintering at higher latitudes. In winter, females take larger prey than males in goshawks and sparrowhawks (Höglund 1964, Opdam 1975).

We found no evidence of intersexual resource partitioning by selection of different types or size of prey in the kestrel. Thus, intersexual food competition is hardly a reason for RSD in this species. In fact, the only documented fitness effect of female size in kestrels during breeding was that small females produced more fledglings in poor vole years (Massemin et al. 2000), when any intersexual food competition should be most severe. This is in agreement with the prediction from the "ingestion rate" hypothesis for RSD (Slagsvold & Sonerud 2007). In fact, there is to the best of our knowledge no unequivocal evidence that females select larger prey than males in breeding raptors, and thus unlikely that intersexual food competition has selected for RSD in raptors. However, as already pointed out (Sunde et al. 2003, Slagsvold & Sonerud 2007), RSD selected and maintained by other factors, for instance reproductive role division may secondarily cause sex-specific resource segregation.

In conclusion, we found that kestrel mates captured prey of the same size, and that the larger size of prey delivered at the nest by the female than the male was an artefact of the male selectively delivering smaller prey directly to the nestlings and larger prey to the female for further processing and finally feeding of the nestlings. The reason for this size-dependent prey allocation by the male was probably the fact that the nestlings became sooner able to ingest smaller prey unassisted, and ingested these more efficiently than larger prey. If such size-dependent prey allocation is general in raptors where the female retrieves prey from the male outside the nest, any inter-sexual difference in prey size previously found by recording prey deliveries at the nest must be re-evaluated. To test the generality of this important pitfall, more data are needed on the extent to which the male allocates prey items directly to the nestlings or indirectly via the female for further processing and feeding, and such data should be collected simultaneously with monitoring prey deliveries at the nest. Failure to find any feeding niche separation between the sexes during breeding would exclude a proposed mechanism for the evolution of RSD in raptors.

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Table 1. Parameter estimates from the best fitted model, with each prey type (lizard, shrew, vole and bird) as intercept, for the probability that a) a prey item delivered at a kestrel nest had been captured by the male (likelihood ratio test; χ^2=11.30, d.f.=1, p <0.001 for nest ID as random effect), b) a prey item captured by the male was delivered directly to the nestlings rather than to the female (likelihood ratio test; χ^2=12.44, d.f.=1, p <0.001 for nest ID as random effect), and c) a prey item was delivered at the nest by the male (likelihood ratio test: χ^2=10.49, d.f.=1, p <0.001 for nest ID as random effect).

	Estimate	SE	z	P
a)				
Lizard vs. shrew	-0.1573	0.3786	-0.416	0.68
Lizard vs. vole	-0.1015	0.3742	-0.271	0.79
Lizard vs. Bird	-0.6022	0.3795	-1.587	0.11
Shrew vs. vole	0.0557	0.3575	0.156	0.88
Shrew vs. Bird	-0.4449	0.3580	-1.243	0.21
Vole vs. Bird	-0.5008	0.3606	-1.389	0.17
b)				
Lizard vs. shrew	1.3552	0.5281	2.566	0.010
Lizard vs. vole	1.6626	0.5284	3.146	0.0017
Lizard vs. bird	2.8257	0.5844	4.835	<0.0001
Shrew vs. vole	0.3072	0.5313	0.578	0.56
Shrew vs. bird	1.4704	0.5662	2.597	0.0094
Vole vs. bird	1.1630	0.5875	1.979	0.048
c)				
Lizard vs. shrew	0.9489	0.4521	2.099	0.036
Lizard vs. vole	1.1945	0.4601	2.596	0.0094
Lizard vs. bird	2.0662	0.5076	4.071	<0.0001
Shrew vs. vole	0.2454	0.4762	0.515	0.61
Shrew vs. bird	1.1172	0.5195	2.150	0.032
Vole vs. bird	0.8716	0.5363	1.625	0.10

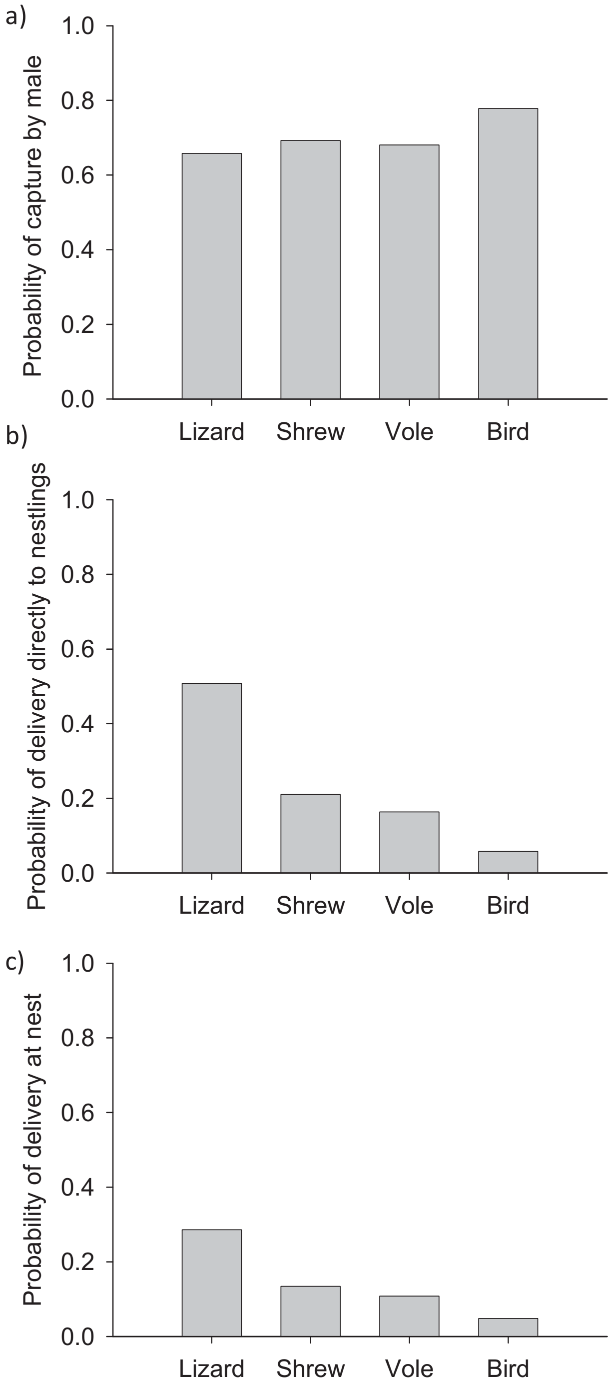

Figure 1. The estimated probability that a prey item delivered at a kestrel nest had been a) captured by the male, b) delivered by the male directly to the nestlings rather than to the female, and c) delivered at the nest by the male, depending on the type of prey (lizard, shrew, vole or bird). Estimates are parameter estimates from the generalized linear mixed effect model (corrected for the random effect of nest ID, see text). See Table 1 for statistical testing of differences between groups.

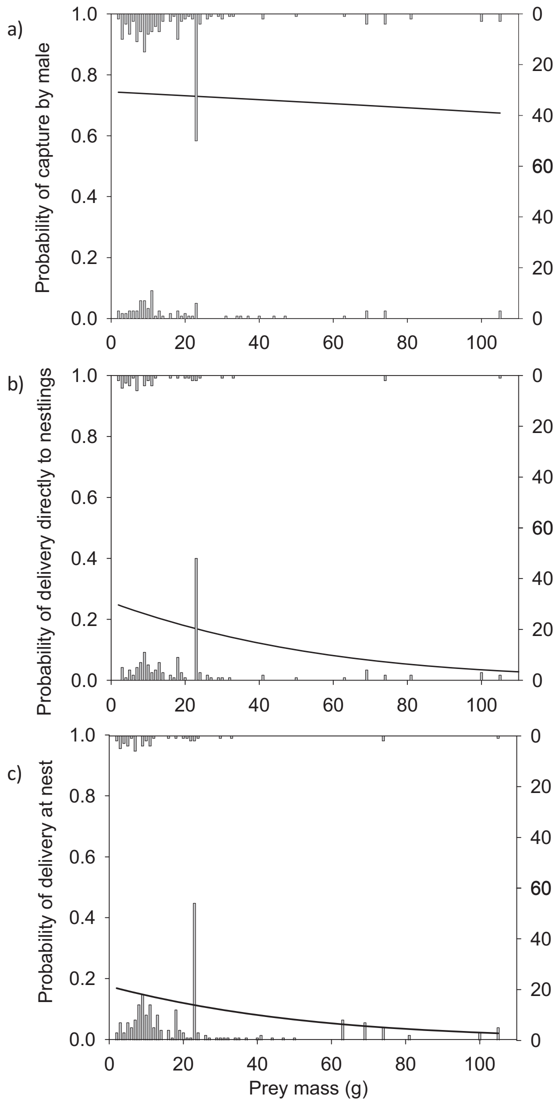

Figure 2. The effect of estimated body mass of a prey item delivered at a kestrel nest on the probability that the item had been a) captured by the male ($y = 1/1+e^{-(1.065 - 0.003x)}$, z = - 0.51, p = 0.61),*)*, b) delivered by the male directly to the nestlings rather than to the female ($y = 1/1+e^{-(-1.070 - 0.023x),}$, z = - 1.82, p = 0.069), and c) delivered at the nest by the male ($y = 1/1+e^{-(-1.552 - 0.022x)}$, z = - 1.94, p = 0.053), with the curves describing the logistic regression models, calculated from the generalized linear mixed effect model parameter estimates (corrected for the random effect of nest ID, see text). The bars (right axis) in the upper row denote the distribution of cases in which the male had captured the prey (a), and the cases in which he delivered the prey he had captured directly to the nestlings (b and c), while the bars in the lower row denote the distribution of cases in which the female had captured the prey (a), the cases in which she received prey from the male (b), and the cases in which she delivered prey at the nest (c).

Paper IV

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The feeding constraint hypothesis: prey preparation as a function of nestling age and prey mass in the Eurasian kestrel

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The feeding constraint hypothesis states that an inability of young nestlings to ingest prey included in the diet of older nestlings and adult birds affects the evolution of parental behaviour, and predicts that the extent of prey preparation would increase with prey size and decrease with nestling age. In the Eurasian kestrel, *Falco tinnunculus*, a small raptor with a wide diet, parents often prepare prey prior to delivery at the nest, most notably by decapitation. We studied this behaviour by video monitoring prey deliveries at 29 nests for a total of about 200 days over 3 years. The probability of a prey item being decapitated prior to delivery differed between prey types and prey sizes; none of the insects or common lizards, *Zootoca vivipara*, and almost none of the shrews (Soricidae) were decapitated, whereas voles (Microtinae) and birds were commonly decapitated. For voles the probability of being decapitated decreased with nestling age, which supports the feeding constraint hypothesis because the nestlings' gape size limit and swallowing capacity would increase with age. For both voles and birds the probability of being decapitated increased with prey body mass, suggesting that kestrel nestlings may be unable to swallow, digest or egest skulls from larger prey. We suggest that the extent to which kestrel parents decapitate prey prior to delivery is an effect of their nestlings' age-dependent swallowing capacity and that the age of the nestlings therefore imposes constraints on the kestrel parents' foraging behaviour.

In a number of bird species the nestlings are fed with prepared or partly digested food because the usual diet of the parents is unsuitable for the nestlings (Clutton-Brock 1991). Such prey preparation is a trade-off between benefits for the nestlings and costs for the parents (e.g. Ponz et al. 1999). Newly hatched and young nestlings can ingest and digest only small and soft food items, and parents usually provide smaller food items to younger than to older nestlings (Slagsvold & Wiebe 2007 and references therein). This feeding constraint has a number of effects on the evolution of parental behaviour (the feeding constraint hypothesis; Slagsvold & Wiebe 2007).

In general, a predator should prepare prey items that are too large to swallow whole (Kaspari 1990). Parts that add most to prey girth should be removed, and more so as prey size increases (Kaspari 1991). In particular, a central place-foraging, single-prey loader, such as a raptor, may decrease the load carried to the nest without decreasing the digestible prey biomass delivered by removing inedible body parts such as feathers, head and scales (Sodhi 1992). Moreover, the raptor may alter its decision to prepare a prey depending on the distance to the central place (Sodhi 1992). The total energy saved would be proportional to the transport distance, and would increase the net rate of energy delivered at the nest (Sodhi 1992). In addition, Rands et al. (2000) proposed that by consuming removed prey parts a parent would reduce the time needed for self-foraging and thus increase overall delivery rate. If the male prepares the prey prior to delivery the female could devote more time to other parental activities, such as feeding and brooding, and the female and nestlings would also be less exposed to ectoparasites from the prey (Rands et al. 2000). Finally, prey preparation may increase the digestibility of the prey by providing increased exposure to digestive enzymes (Kaspari 1991).

In raptors (hawks Accipitriformes, falcons Falconiformes and owls Strigiformes) parents often remove the head of the prey prior to providing the remaining body to the nestlings. This decapitation is most likely to be conducted on the capture site or near the nest (Newton 1979). The size of the skulls of mammals and birds may exceed the swallowing capacity of nestlings below a critical age. If

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so, the frequency of decapitation of prey delivered to nestlings would decline with nestling age. In addition, as skulls are often egested as pellets in raptors (Village 1990; Duke et al. 1997), a skull has to pass the gape of the nestlings twice, in contrast to what is the case in passerine birds (Kaspari 1990, 1991; Barba et al. 1996; Ponz et al. 1999). Furthermore, ingested skulls of large voles and birds may be too large for the nestlings to form as pellets and to egest. If not egested, the skulls have to pass through the whole gastrointestinal tract (Duke et al. 1997), which will impede digestion or even be harmful. However, a large proportion of skulls and bones are in fact digested in falcons, in contrast to owls, which have less gastric acidity (Bond 1936; Duke et al. 1975, 1997; Hoffman 1988). Moreover, the digestion of bones may be less efficient in young nestlings than in older nestlings and adults. Therefore, raptors may more frequently decapitate prey prior to delivery for younger nestlings than for older nestlings, and more frequently when the prey is large than when it is small. These patterns do not seem to have been sufficiently recognized in earlier studies of prey preparation in breeding raptors (e.g. Sodhi 1992; Rands et al. 2000).

In this study we focused on factors that influence the probability of decapitation of prey delivered at the nest in the Eurasian kestrel, *Falco tinnunculus*, hereafter called kestrel, which is a small raptor (male body mass about 200 g) taking a variety of prey including voles, shrews, birds, lizards and insects (Village 1990; Fargallo et al. 2003), and regularly preparing prey by decapitating it prior to delivery at the nest (Pikula et al. 1984; Village 1990). During the first half of the 4-week nestling period the male usually provides most of the prey, which he delivers to the female, which then dismembers the prey and feeds it to the nestlings. Later on, the female may also hunt, and as the nestlings become able to feed unassisted they are left to consume prey on their own (Village 1990; Fargallo et al. 2003).

We studied prey delivery in breeding kestrels by use of video monitoring, to test predictions on prey preparation patterns derived from the feeding constraint hypothesis (Slagsvold & Wiebe 2007), that is, that young nestlings would be unable to swallow skulls because of the gape size limit (e.g. Saunders et al. 1995; Forsman 1996; Nilsson & Bronmark 2000). Since gape size limit and swallowing capacity is age dependent we predicted that the probability of decapitation is a function of nestling age and prey size. Thus, the probability of decapitation would decrease with nestling age and larger prey would be more likely to be decapitated than smaller prey.

METHODS

Study Area and Species

The study was conducted in the boreal and hemiboreal zones in Trysil municipality, Hedmark county, southeast Norway (61°07′–61°31′N, 12°00′–12°48′E) during June and July in 2003, 2005 and 2007. Here, more than 100 pairs of the kestrel breed in artificial nestboxes each year, of which we monitored nine in 2003, 10 in 2005 and 10 in 2007. The nestboxes had an open front, and were situated 5–15 m above ground in trees located in bogs or clear-cuts at altitudes of 300–700 m. In our study area, the kestrel is a migrant that arrives in April and May. In western Finland (63°N) the kestrel is also a migrant, and only 25% of the males and 8% of the females reuse the same nest site in successive years (Tolonen & Korpimäki 1995). In Scotland (55°N), where the kestrel is partly resident, 29% of males and 18% of females reuse the same nest site in successive years (Village 1990). Thus, although we filmed one nestbox in both 2003 and 2005 and one in both 2003 and 2007, different individuals were probably involved. Therefore, when treating breeding pairs as the statistical unit, we regarded 29 as the sample size.

Video Monitoring

We checked the nests at least twice before the video monitoring to determine hatching date. In 2003 and 2005 each brood was filmed for 2 days, except one in 2003, which was filmed for 1 day only. In 2003, these days were 2 weeks apart; the nests were filmed first when the last-hatched nestling was on average ± SE 12.3 ± 0.7 days old (range 8–15), and second when it was 25.9 ± 0.6 days old (range 23–28). In 2005 the nests were filmed on 2 subsequent days, starting when the average age of the last-hatched nestling was 12.6 ± 0.8 days (range 8–16), with one exception: in one of the nests the second filming was conducted 2 days after the first. Brood size was on average 5.0 ± 0.3 (range 4–7) in 2003, and 3.1 ± 0.5 (range 1–5) in 2005. In 2007, continuous monitoring was done to cover a larger part of the breeding period, starting when the average age of the last-hatched nestling was 10.2 ± 0.6 days (range 8–12), and ending when it was 26.7 ± 0.5 days (range 24–29). In 2007 brood size was 5.0 ± 0.3 (range 3–6).

In 2003, prey deliveries were recorded with a Canon MV550i digital camcorder, which was mounted on top of the nestbox with the lens pointed through the roof and towards the open front of the box, so that the prey was in view when the adult kestrel arrived. To habituate the kestrels to filming, a dummy camcorder was mounted in the same position 1–2 days before filming. We used Mini DV cassettes, which lasted 2 h 40 min in long-play mode. A Canon Battery Pack BP-535 (7.4 V, 3500 mAh) was used for the power supply. Each brood was videorecorded for an average of 10 h 40 min (four cassettes) between 0600 and 1700 hours each day.

In 2005, each of the 10 original nestboxes was replaced with a plywood nestbox 2–4 days prior to filming, allowing the kestrels to habituate. A camera-top made of plywood was put on top of the nestboxes, and was fixed in place 1 day prior to filming. This top contained a wired CCTV camera lens, which was positioned at such an angle that the prey was in view when the parents delivered it to the nestlings. A connection made of 50 m of video cable between the lens and a Canon MV850i digital camcorder allowed monitoring and recording of prey deliveries from a hide on the ground. Hence, the cassettes could be switched in the hide without disturbing the kestrels. A sealed 12 V lead battery (10 Ah) with a voltage converter (from 12 to 8.4 V) was used for the power supply to the camcorder. We used Mini DV cassettes, which lasted 2 h in long-play mode. Each brood was filmed for an average of 10 h (five cassettes) from 0600 to 1600 hours each day.

In 2007, each of the 10 original nestboxes was replaced with a nestbox specially made for filming. Inside the nestbox, a CCD camera lens was placed in the back corner underneath the roof, pointing towards the nestbox entrance. The camera was connected with a 10 m video cable to a mini digital video recorder (DVR) located on the ground, which stored data on SD cards. For further details, see Steen (2009).

Measuring Delivered Prey

We identified and classified each prey item on delivery (i.e. insect, common frog, *Rana temporaria*, common lizard, *Zootoca vivipara*, shrew (Soricidae), vole (Microtinae) or bird), scored it as decapitated or not, and determined whether it was delivered by the male or the female kestrel (see Supplementary Material). In some cases ($N = 26$), the parent landed on the nestbox with a prey item without delivering it to the nestlings, flew off with the item, returned later and delivered apparently the same item to the nestlings. We counted such potential duplicate deliveries as only one if the time between departure and arrival was ≤30 min. In one such case a vole was first whole but was decapitated when the kestrel arrived with it later, and was scored as decapitated.

Of the 4209 recorded prey deliveries, nine were classified as insects, one as a frog, 168 as lizards, 475 as shrews, 3108 as voles and 279 as birds, whereas 169 were unclassified. Mode of decapitation was assessed for all the insects and lizards, 463 of the shrews, 2870 of the voles and 263 of the birds. However, only decapitation of voles and birds was analysed further since none of the insects or lizards, and very few shrews, were decapitated.

We analysed the data subset from 2003 and 2005 in more detail to assess the effect of prey body mass on the probability of decapitation. This was done for voles and birds only, since too few items of the other prey types were decapitated on delivery. Of the 367 prey items recorded delivered in 2003 and 2005, 79 were classified as voles and 129 as birds.

The body mass of lizards and small mammals has a relatively high intraspecific variation (Smajda & Majlath 1999; Norrdahl & Korpimäki 2002). Therefore, we estimated the body mass of each lizard and small mammal prey item delivered by the kestrels, rather than using an average mass for each species as has been done in previous studies (Fargallo et al. 2003; Laaksonen et al. 2004). We measured delivered prey items on a monitor as described by Steen (2004) and Løw (2006). For common lizards, we used the regression model by Van Damme & Vanhooydonck (2001): log (body mass) $= -1.767 + 3.201 \times \log$ (SVL), where SVL is snout–vent length. For small mammals we used a regression between body mass and size on the monitor obtained for specimens of the same species with known size and mass (Steen 2004; Løw 2006). As the head of decapitated voles was estimated to weigh 16.5% of the total body mass (Asakskogen 2003), we divided the estimated body mass of decapitated voles by 0.835 to obtain the body mass prior to decapitation.

The body mass of birds has a relatively small intraspecific variation; therefore a mean value for each prey species was obtained from data most pertinent to the breeding season in Fennoscandia (Cramp & Simmons 1980, 1983; Cramp 1985, 1988, 1992; Cramp & Perrins 1993, 1994a, b; Matthysen 1998; Selås 2001). If a bird was identified to genus only, as for instance many thrushes (*Turdus*) were, we calculated an average body mass of the possible species alternatives. For passerines, juveniles were given the same body mass as adults, whereas for grouse and shorebirds, the body mass of juveniles was estimated from form and relative size on the video frame. The estimated body mass of avian prey delivered at the nests is listed elsewhere (Steen 2004; Løw 2006).

For three voles and six birds in 2003 and 2005 the mode of decapitation could not be determined. Furthermore, for another 26 voles and eight birds it was not possible to estimate the prey body mass. Thus, the total number of prey items we used for the analysis of effects of prey body mass was 165 (50 voles and 115 birds).

Statistics

Statistical analyses were performed with the software R version 2.8.1 (R Development Core Team 2008), using the generalized linear mixed-effect model by the Laplace approximation in the lme4 package (Pinheiro & Bates 2000). We tested whether the probability that a prey was decapitated prior to delivery at the nest depended on nestling age, and whether this effect differed between voles and birds. Explanatory variables were nestling age, prey type (vole or bird), and the interaction between nestling age and prey type, with breeding pair and year as random factors. The interaction term was included because our purpose was to test whether there was a difference in the probability of decapitation between the two prey types, and whether this difference changed as the nestlings grew older. Nestling age (age of the last-hatched brood member) would give an indirect measure of the feeding capacity of the nestlings, that is, their gape size, pellet formation, egestion and digestion. Breeding pair was included as a random factor to control for a possible variation caused by individual differences. Year was included as a random factor to control for potential variation between years in conditions that may influence the probability of decapitation.

We analysed the data from 2003 and 2005 in more detail by testing whether the probability that a prey item was decapitated prior to delivery at the nest depended on prey body mass in addition to nestling age, and whether these effects differed between voles and birds. Explanatory variables were prey body mass, prey type (vole or bird), nestling age, the interaction between nestling age and prey type, and the interaction between prey body mass and prey type, with breeding pair and year as random factors. The two interaction terms were included to test whether the probability of decapitation differed between the two prey types, and whether this difference changed as prey body mass and nestling age changed.

In both tests, the sex of the parent delivering the prey, and the interaction between nestling age and the sex of the parent delivering the prey, were considered as cofactors. Since the male provides most prey during the first 2 weeks of the nestling period and the female assists later on (Village 1990), a reduction in the proportion of decapitated prey as the nestlings age may be caused by the female being less inclined to decapitate prey. Therefore, the interaction term was included to control for a possible intersexual difference in prey-handling behaviour, and whether this intersexual difference changed as nestlings aged. Furthermore, in both tests, brood size was considered as a cofactor. The cofactors were included only when significant at $\alpha = 0.10$.

We used log likelihood ratio tests to check for the significance of random effects. We compared the two fitted models with different specifications of the random effects and checked whether removal of a random effect caused a significant decrease in the log likelihood ratio (Bolker et al. 2009). Breeding pair was kept as a random effect in the model regardless of its significance value to control for possible variation caused by individual differences. Year as a random effect was included in the final model only when significant at $\alpha = 0.10$.

Figures were constructed by using the Sigma-Plot version 9.01 graphics package (SPSS Inc., Chicago, IL, U.S.A.). Estimates are presented as mean ± SE.

Ethical Note

The study was performed under licence from the Directorate for Nature Management. To avoid the risk of parents deserting the brood or nestlings getting cold because of a lack of brooding, the camera installations and nestbox replacement were done when the oldest nestlings were at least 1 week old. At this stage the nestlings are able to keep warm without assistance from the female (Village 1990). Furthermore, in 2005 the video cassettes could be switched on the ground without disturbing the kestrels, and the method applied in 2007 allowed several days between successive visits for SD card replacement, which took only a minute (see Steen 2009). The kestrels were tolerant towards human disturbance and resumed their parental activities quickly after the installation procedure.

RESULTS

The effect of nestling age on the probability that a prey item was decapitated prior to delivery at the nest differed significantly between voles and birds; the probability of a prey item being decapitated decreased significantly with nestling age for voles, but not for birds (Table 1, Fig. 1). The female was not less inclined than

Table 1
Probability of decapitation of prey prior to delivery at kestrel nests as a function of nestling age

	Estimate	SE	z	P
(Intercept)	0.568	0.317	1.794	0.073
Nestling age	−0.058	0.009	−6.309	<0.001
Prey type (bird)	−0.628	0.594	−1.058	0.290
Parent sex (male)	0.056	0.434	0.130	0.897
Nestling age*Prey type	0.100	0.034	2.960	0.003
Nestling age*Parent sex	−0.050	0.024	−2.135	0.033

Parameter estimates of the selected generalized linear model with vole and female as intercept for the variables prey type and parent sex, and with breeding pair and year as random effects, based on data from 2003, 2005 and 2007 (3133 prey items, 29 breeding pairs).

the male to deliver decapitated prey, but the probability of decapitation decreased significantly more slowly with nestling age for prey that the female delivered than for prey that the male delivered directly at the nest (Table 1, Fig. 1). Both random effects, breeding pair and year, were kept in the model (likelihood ratio test: breeding pair: $\chi^2_1 = 58.28$, $P < 0.001$; year: $\chi^2_1 = 3.33$, $P = 0.07$). Brood size did not contribute significantly to the model.

None of the insects ($N = 9$) or lizards ($N = 168$) were decapitated prior to delivery, compared to 1.2% of the shrews ($N = 463$), 52.2% of the voles ($N = 2870$) and 63.9% of the birds ($N = 263$). Based on data from 2003 and 2005, estimated body mass of prey prior to delivery at the nest was 0.2 g ($N = 9$) for insects, 5.3 ± 0.3 g ($N = 54$) for lizards, 9.6 ± 0.3 g ($N = 64$) for shrews, 20.3 ± 1.3 g ($N = 51$) for voles, and 37.8 ± 2.5 g ($N = 118$) for birds. The range of estimated body mass was 1.5–10.8 g for lizards, 4.0–16.0 g for shrews, 6.0–47.0 g for voles, and 9.0–105.0 g for birds.

For the data from 2003 and 2005, there was a significant effect of prey body mass on the probability that a prey item was delivered decapitated, and the effect differed significantly between voles and birds (Table 2). For both prey types the probability of decapitation increased with prey body mass, but the increase was significantly faster for voles than for birds (Figs 2, 3). As was the case in the test for the whole data set the probability of a prey item being decapitated decreased significantly with nestling age for voles, but not for birds. The random effects, breeding pair and year, did not contribute significantly to the model. However, breeding pair was still included in the model to control for a possible variation caused by individual differences (likelihood ratio test: $\chi^2_1 = 0.86$, $P = 0.36$). For a given prey body mass, the probability of decapitation was lower for voles than for birds, except when heavy voles were delivered to young nestlings (Figs 2, 3). However, for the heaviest avian prey item (105 g) the probability of decapitation approximated the value for the heaviest vole (47 g) delivered to young nestlings (Fig. 2). Brood size, parent sex, and the interaction terms

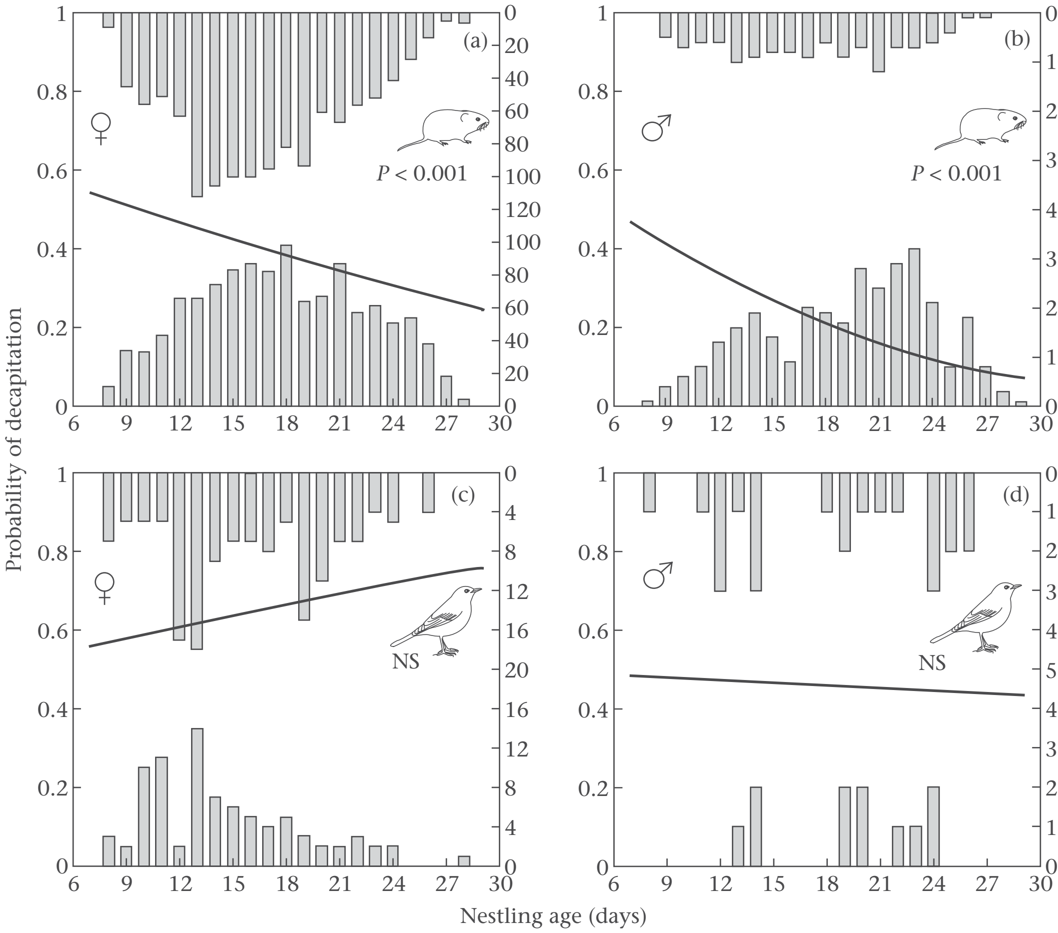

Figure 1. The probability that a prey item was decapitated prior to delivery at kestrel nests as a function of nestling age, with the curve describing the logistic regression model, calculated from the glm parameter estimates (scale on the left axis). Upper bars denote prey delivered decapitated and lower bars denote prey delivered whole (scale on the right axis). Based on data from 2003, 2005 and 2007. (a) The probability that a vole was delivered decapitated by the female: $y = 1/1 + e^{-(0.57-0.06x)}$ ($z = -6.31$, $P < 0.001$). (b) The probability that a vole was delivered decapitated by the male: $y = 1/1 + e^{-(0.62-0.11x)}$ ($z = -4.91$, $P < 0.001$). (c) The probability that a bird was delivered decapitated by the female: $y = 1/1 + e^{-(-0.06+0.04x)}$ ($z = 1.26$, $P = 0.208$). (d) The probability that a bird was delivered decapitated by the male: $y = 1/1 + e^{-(-0.004-0.009x)}$ ($z = -0.24$, $P = 0.811$).

Table 2
Probability of decapitation of prey prior to delivery at kestrel nests as a function of prey body mass and nestling age

	Estimate	SE	z	P
(Intercept)	−0.876	1.575	−0.556	0.578
Prey body mass	0.138	0.052	2.621	0.009
Nestling age	−0.223	0.102	−2.192	0.028
Prey type (Bird)	−0.021	1.793	−0.011	0.991
Prey body mass*Prey type	−0.108	0.053	−2.017	0.044
Nestling age*Prey type	0.229	0.119	1.920	0.055

Parameter estimates of the selected generalized linear model with vole as intercept for the variable prey type, and with breeding pair as random effect, based on data from 2003 and 2005 (165 prey items, 19 breeding pairs).

between parent sex and nestling age and between parent sex and prey body mass, did not contribute significantly to the model.

DISCUSSION

The kestrels were less likely to decapitate voles prior to delivery with increasing nestling age, that is, with nestling developmental stage. This is consistent with the feeding constraint hypothesis. Similarly, Barba et al. (1996) found a negative relationship between the degree of prey preparation and nestling age in the great tit, *Parus major*. In the mountain chickadee, *Parus gambeli*, the preparation of prey declined with nestling age during the first half of the nestling period (Grundel & Dahlsten 1991). The reason why the probability of decapitation of birds was not associated with nestling age in the kestrel may be because many decapitated birds were thrushes (*Turdus*), which are relatively large (about 70–100 g) compared to kestrels, and thus may have skulls exceeding the gape size limit of kestrel nestlings regardless of the age of the latter. Small birds may have soft skulls which are easier to crush and thereby less likely to exceed the nestlings' gape size limit, and thus easier to egest or digest, even for young nestlings.

The probability that a prey item delivered at the nest was decapitated did not differ between the kestrel mates overall, but it decreased more slowly with nestling age for the female than for the male. Because of the separate parental roles, with the female being responsible for dismembering and feeding the prey to the nestlings and thus being more attached to the nest (Village 1990), the female may be less time constrained than the male and may therefore invest in prey preparation for a longer period.

The percentage of prey items decapitated prior to delivery at the kestrel nests was nil for insects and lizards, negligible for shrews, but substantial for voles (52%) and birds (64%). Thus, across prey types the probability of decapitation increased with prey size.

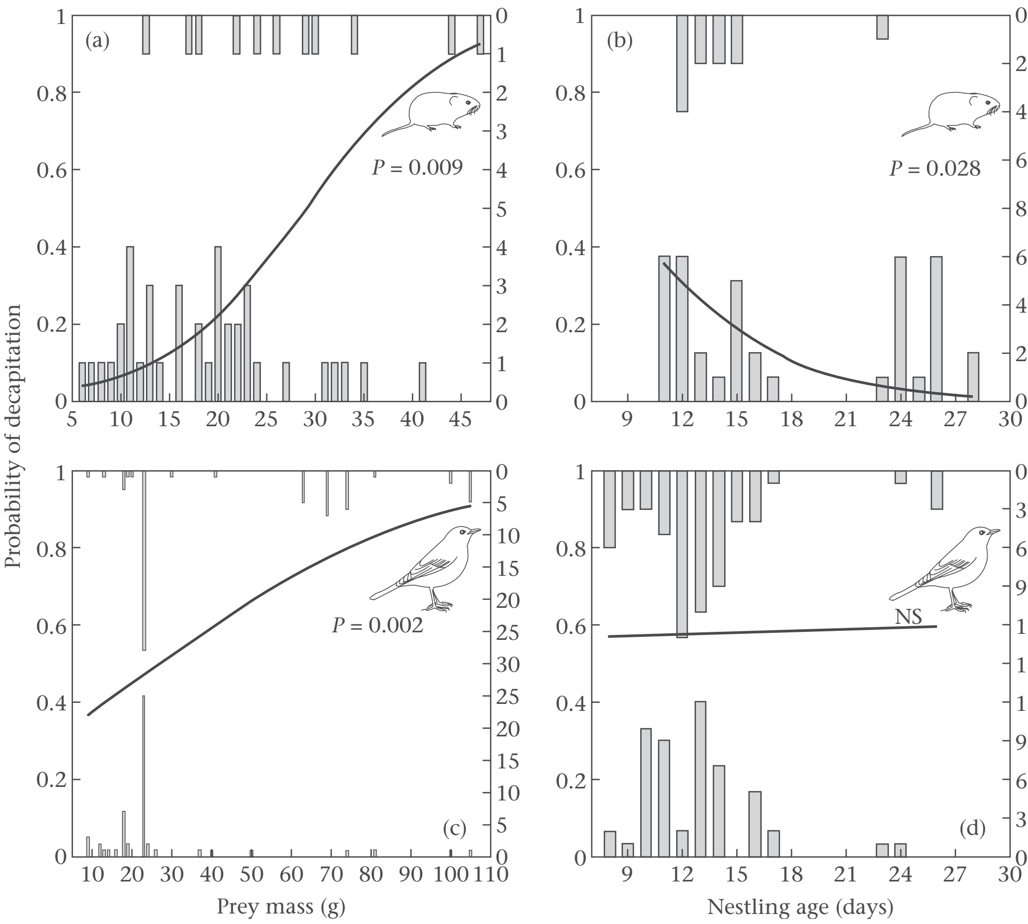

Figure 2. The probability that a prey item was decapitated prior to delivery at kestrel nests as a function of prey body mass for an average nestling age, and as a function of nestling age for an average prey body mass, with the curve describing the logistic regression model, calculated from the glm parameter estimates (scale on the left axis). Upper bars denote prey delivered decapitated and lower bars denote prey delivered whole (scale on the right axis). Based on data from 2003 and 2005. (a) The probability that a vole was delivered decapitated as a function of prey body mass when nestlings were 14 days old: $y = 1/1 + e^{-(-4.00+0.14x)}$ ($z = 2.62$, $P = 0.009$). (b) The probability that a vole weighing 20 g was delivered decapitated as a function of nestling age: $y = 1/1 + e^{-(1.88-0.22x)}$ ($z = -2.20$, $P = 0.028$). (c) The probability that a bird was delivered decapitated as a function of prey body mass when nestlings were 14 days old: $y = 1/1 + e^{-(-0.82+0.03x)}$ ($z = 3.03$, $P = 0.002$). (d) The probability that a bird weighing 38 g was delivered decapitated as a function of nestling age: $y = 1/1 + e^{-(0.24+0.006x)}$ ($z = 0.08$, $P = 0.934$).

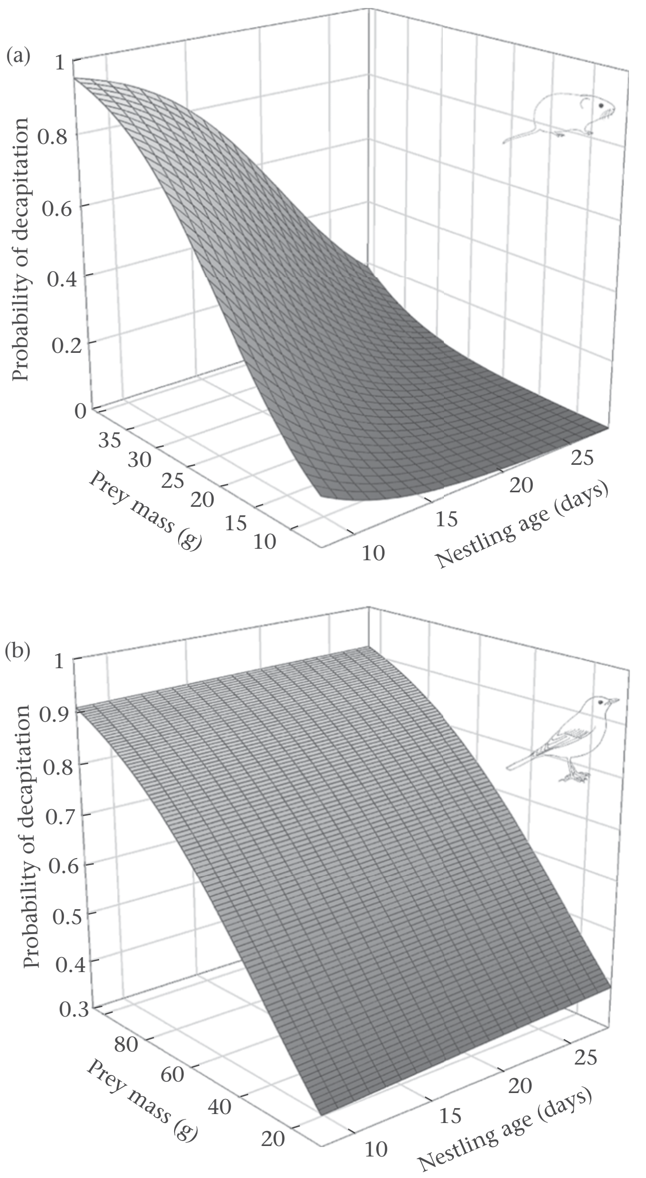

Figure 3. The probability that a prey item was decapitated prior to delivery at kestrel nests as a function of prey body mass and nestling age, with the plane describing the complete logistic regression model, calculated from the glm parameter estimates. (a) Voles. (b) Birds.

Pikula et al. (1984) found that 50% of the voles ($N = 53$) and 71% of the birds ($N = 59$) delivered by kestrels at the nest were decapitated, which is very similar to our figures.

The probability that voles and birds were delivered decapitated increased with prey body mass, in addition to the effect of nestling age. This is consistent with the feeding constraint hypothesis. A similar pattern has been observed in passerines, which are more likely to prepare larger prey items than smaller ones (Sherry & McDade 1982; Kaspari 1990; Barba et al. 1996; Ponz et al. 1999). We found that the kestrels more often decapitated birds than voles prior to delivery at the nest. However, this was partly because the birds were on average heavier than the voles, as the probability of decapitation was in fact higher for larger voles (30–40 g) than for birds of the same mass when the nestlings were young. In terms of restricted gape size or increased risk of injury while feeding (Kaspari 1991; Duncan & Nero 1998), the head of a vole may in general be less difficult for the nestlings to swallow whole, egest or digest than the head of a bird of the same body mass owing to the shape of the head and the bill of the latter, but this may not be the case for larger voles delivered to small nestlings.

In terms of travelling costs when carrying prey to the nest, removal of the head of birds may reduce potential drag because the prey would become more aerodynamically shaped (Rands et al. 2000). The head of a large bird may contribute more to air resistance than the head of a large vole. Therefore removing the head of a bird would be more likely to reduce drag and increase flight speed (Norberg 1981) than removing the head of a vole prior to transport from the capture site to the nest.

The fact that the probability of decapitation increased with prey body mass is consistent with the hypothesis that a central place-foraging, single-prey loader may decrease the load carried to the nest, without decreasing the digestible prey biomass delivered, by removing inedible body parts (Sodhi 1992). However, this hypothesis can hardly explain why the probability of decapitation of voles decreased with nestling age. Also, given that the parent raptor consumed removed prey parts to reduce the time needed for self-foraging (see Rands et al. 2000), the total travel cost would be approximately the same. We have no data on travel distance, but if prey were more likely to be decapitated prior to transport with longer distance between the capture site and the nest (Sodhi 1992), our finding that voles were less likely to be decapitated as the nestlings grew older would mean that voles were captured closer to the nest as the season progressed. We do not find such a pattern very likely, because any resource depression effect of the kestrels' hunting combined with an increasing energy need of older nestlings would rather force the parents to hunt further from the nest as the nestlings grow.

The probability that a prey item was delivered decapitated differed between breeding pairs, and tended to differ between years. The relative cost of prey preparation for the parents may vary inversely with the abundance of voles and thus be high at low vole abundance, because a long time is needed to search for prey then. Furthermore, prey parts with low profitability for the nestlings, such as large skulls that are difficult to swallow and digest, may be more often included in the diet of the nestlings at low vole abundance owing to food scarcity. The variation in probability of decapitation between breeding pairs may be caused by not only ecological differences between territories, but also consistent individual differences in prey-handling behaviour. Such behavioural syndromes or animal personalities have been documented in a variety of animals, including birds (e.g. Garamszegi et al. 2009; Kontiainen et al. 2009).

Our results indicate that when the kestrel parents decided whether to decapitate a prey prior to delivery at the nest, their preparation of voles and birds was similarly affected by prey body mass, but differently affected by the age of their nestlings. However, we may have underestimated the effect of nestling age on prey preparation because, for ethical reasons, our study was conducted when the nestlings were more than 8 days old. If we had included the whole nestling period, we may have found an effect of nestling age also on the probability of decapitating avian prey.

We conclude that decapitation of prey in kestrels is likely to be an effect of their nestlings' age-dependent gape size limit and swallowing capacity, in accordance with the feeding constraint hypothesis. This would impose constraints on the foraging behaviour of the kestrel parents.

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at doi:10.1016/j.anbehav.2010.04.015.

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Paper V

Prey delivery rates as estimates of prey consumption by Eurasian kestrel (*Falco tinnunculus*) nestlings

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Abstract

In altricial birds, the type of prey selected by the parents for their nestlings may affect the allocation of time and energy spent on hunting, preparing prey and feeding the nestlings, which may in turn affect the rate of provisioning. Raptors take relatively large prey items, which facilitates the quantification of rates of prey items and prey mass delivered to nestlings. Estimates of rates of prey delivery in raptors are nevertheless few, and have been based on direct observations from a hide in combination with analyses of prey remnants and regurgitated pellets. To obtain better estimates, we video monitored prey deliveries at 55 nests of the European kestrels (*Falco tinnunculus*). Of the 2282 prey items recorded delivered, voles were most abundant by number, followed by birds, shrews and lizards, while insects and frogs were rare. An average brood size of 4.3 nestlings was estimated to consume 18.3 g^{-h}, hence a nestling consumed on average 4.2 g^{-h}. This is equivalent to 67.8 g^{-d}, given an average daily activity period of 16.1 h. The estimated delivery rate of prey items required to feed an average brood in our study was 90.5^{-h} if the kestrels had provided only insects, and 3.4, 1.9, 0.8 and 0.5 if they had provided only lizards, shrews, voles or birds, respectively. This corresponds to one prey delivery per 40 sec if feeding solely on insects, and one per 18, 32, 75 and 120 min if feeding solely on lizards, shrews, voles or birds, respectively. We argue that kestrels in the boreal forest would be unable to raise an average brood solely on insects or lizards, unlikely to do so solely on shrews or avian prey, but able to do so solely on voles in a vole peak year.

Keywords: brood size, Eurasian kestrel, *Falco tinnunculus,* nestling, prey consumption, prey delivery rate, prey mass

Introduction

In altricial birds the type of prey selected by the parents for their nestlings affects the allocation of time and energy spent on food collection, preparation and feeding (e.g. Slagsvold and Sonerud 2007, Slagsvold and Wiebe 2007, Steen et al. 2010a,b). Parents are assumed to maximize the total delivery to the brood, given the time constraints set by self-feeding and hunting (Ydenberg 2007), and to capture prey that most optimally covers the daily energy needs of the nestlings (Fagerström et al. 1983 and references therein). Because the nestlings' probability of survival depends on the parental investment, the parents must trade the costs and benefits of their investment to maximize their reproductive fitness. Hence, the parents must trade between offspring quality and quantity (Morris 1985 and references therein). Raptors, i.e. hawks (Accipitriformes), falcons (Falconiformes) and owls (Strigiformes), take relatively large prey for their size, and need to allocate a significant amount of time to prepare the prey and feed the nestlings (Newton 1986, Slagsvold and Sonerud 2007, Steen et al. 2010a,b). Hence, raptors are suitable model organisms for a study on food provisioning.

A well studied avian raptor taking a wide spectrum of prey types is the Eurasian kestrel (*Falco tinnunculus*), hereafter referred to as the kestrel, an open country raptor which feeds mainly on ground dwelling animals like voles (Cricetidae), shrews (Soricidae) and lizards, and also on birds and insects (Village 1990). The kestrel shows both a functional and a numeric response to voles. During years with low vole abundance kestrels feed on a wider variety of prey including more birds and insects (Fargallo et al. 2003), and usually have a reduced brood size (Wiebe et al. 1998), most likely to increase the chance to fulfil the energy demand of the nestlings.

Estimates of rate of prey delivery in raptors in general, and in the kestrel in particular, are few and have been based on direct observations from a hide in combination with analyses of prey remnants and regurgitated pellets, e.g. Masman et al. (1989), Holthuijzen (1990), Olsen et al. (1998) and Geng et al. (2009). In this study, we provide more accurate estimates of the rate of prey delivery in the kestrel, by using data from video monitoring of prey deliveries and prey handling in the nestling period (Lewis et al. 2004). We use these estimates to quantify the rate of prey consumption by the nestlings, and finally to predict the rate of prey items necessary to deliver for the different types of prey to raise a kestrel brood.

Methods

We used video to monitor prey deliveries at 55 kestrel nests in the boreal and hemi-boreal zones in Hedmark county, south-eastern Norway (61º07´-61º32´ N; 11º56´-12º48´ E) during June - July in 2003 and 2005-2009. The average brood size at the time of filming was 4.3 ± 0.2 (n=55). The study area covers c. 1200 km^2 and is dominated by intensively managed coniferous forest with a high proportion of clear-cuts interspersed with bogs, and with only negligible patches of farmland.

Video monitoring

The 55 video monitored nests were located in 47 different nest boxes. Six nest boxes were monitored for two years and one for three years. Of the nest boxes monitored for two years, three were monitored in subsequent years, one was monitored three years apart, and two were monitored five years apart. The nest box monitored for three years was first filmed two years apart and then three years apart. In our study area, the kestrel is a migrant that arrives in April and May. Also in western Finland (63°N) the kestrel is a migrant, and only 25% of the males and 8% of the females reuse the same nest site in successive years (Tolonen and Korpimäki, 1995). In Scotland (55°N), where the kestrel is partly resident, 29% of males and 18% of females reuse the same nest site in successive years (Village, 1990). Applying these high turnover rates to our reuse of boxes for filming suggests that one individual or less of each sex would have been filmed at two nests. We therefore assumed that few, if any, adult kestrels were involved in more than one of our 55 monitoring sessions, and breeding pairs were treated as the statistical unit.

In 2003, nine nests were filmed on two separate days, first when brood age (i.e. the age of the last hatched nestling) was 12.3 ± 0.7 days (mean ± SE, range 8-15), and second when it was 25.9 ± 0.6 days (range 23-28). In 2005, ten nests were filmed on two subsequent days, starting when brood age was 12.6 ± 0.8 days (range 8-16; at one nest the second filming was conducted two days after). In 2006, six nests were filmed on two subsequent days, starting when brood age was 13.3 ± 0.6 days (range 12-15; at one nest the second filming was conducted two days after). In 2007, ten nests were filmed continuously for three subsequent days, starting when brood age was 10.2 ± 0.6 days (range 8-12). In 2008, eleven nests were filmed continuously for three subsequent days, starting when brood age was 10.9 ± 0.4 days (range 9-13; at one nest the second filming was conducted two days after). In 2009, nine nests were filmed continuously for three subsequent days, starting when brood age was 11.3 ± 0.4 days (range 10-14). Brood size was on average 5.0 ± 0.3 (range 4-7) in 2003, 3.1 ± 0.5 (range 1-5) in 2005, 4.5 ± 0.3 (range 3-5) in 2006, 5.0 ± 0.3 (range 3-6) in 2007, 5.0 ± 0.3 (range 3-6) in 2008, and 3.4 ± 0.4 (range 2-5) in 2009. Brood size varied significantly among years (ANOVA, $F = 5.27$, $df = 5$, $p < 0.001$).

In 2003, food provisioning was recorded with a digital camcorder. The camcorder was mounted on the top of the nest boxes with the lens pointed through a hole in the roof and towards the open front of the nest box. To habituate the kestrels to filming a dummy camcorder was mounted in the same position as the real camcorder 1 - 2 days before filming. Each brood was video recorded for an average of 10 h 40 min (between 6 am and 5 pm) in both periods, using 80 minutes mini digital cassettes, lasting 2 h 40 min in long play mode. A feeding session was only interrupted during tape change. In 2005, the ten original nest boxes were replaced with nest boxes made specifically for filming, 2-4 days prior to filming to allow the kestrels to habituate. A specially made camera-top of plywood was fitted to the nest boxes at all nests, and was placed on the nest box one day prior to filming. This top contained a wired CCTV camera lens. The lens was positioned in such an angle that the prey was in view from arriving of the parent to feeding. Power supply to the lens was provided by a 12 V lead battery placed on the ground at the base of the nest tree. A connection made of 50 m modified video cables between the lens and a camcorder allowed monitoring and recording of prey deliveries and handling from a hide on the ground. This allowed for the cassettes to be switched in the hide without any disturbance to the kestrels. Digital mini dv cassettes were used, which lasted 2 h in long play mode. Each brood was filmed for 10 h from 06.00 am and 04.00 pm each day. In 2006, the same nest-box setup was used as in 2005, but instead of using a camcorder as a recording unit we used a time lapse video recorder (VHS) and a hard disk recorder (HDD) in combination with an external camera for the former and a mini-dv for the latter. Each brood was filmed for c. 11.5 h (between 6 am and 10 pm). In 2007 and 2008 the ten original nest boxes were replaced with nest boxes made specifically for filming. Inside the nest box a CCD camera was placed in the top back corner and pointed towards the entrance of the nest box. The camera was mounted with a wide angle lens to cover a broad view inside the nest box, and was connected with a video cable to a mini digital video recorder (mini DVR) on the ground, which stored data on SD cards. For details see Steen (2009). In 2009, the equipment described by Steen (2009) was used, but instead of replacing the original nest box with a nest box with the camera inside we used a special-made camera stand, which was placed into the original nest box while an observer watched the monitor on the ground to ensure a correct camera view. For the data in 2007, 2008 and 2009, three days of continuous monitoring were used for each brood (c. 61.5 h, subtracting the period of 3.5 h without prey deliveries for each night). Different set-ups between years were a consequence of technical improvements, and aall set-ups were equally capable of recognizing prey items delivered at the nests.

We identified each prey item delivered by the kestrels to type, i.e. whether it was a common lizard (*Zootoca vivipara*), shrew (*Sorex* sp.), *Myodes* vole (bank voles (*Myodes glareolus*) or grey sided voles (*Myodes rufocanus*)), *Microtus* vole (field vole (*Microtus agrestis*) or root vole (*Microtus oeconomus*)), wood lemming (*Myopus schisticolor*), bird, frog (*Rana* sp.), insect, or remains from mountain hare (*Lepus timidus*).

Prey mass estimation

We estimated the body mass of each prey item recorded delivered in 2003 and 2005 (see below). These estimates were used to calculate a mean body mass for each prey type, and were then used for the whole data set. If kestrels are prey size selective when hunting small mammals, as shown by Masman et al. (1986), our estimates are more reliable than mean values obtained solely from the literature. The body mass of small mammals and lizards has a relatively high intra-specific variation (Norrdahl and Korpimäki 2002, Smajda and Majlath 1999, Hansson 1992, Yoccoz and Mesnager 1998). Therefore, we estimated the body mass of each lizard and small mammal item delivered by the size of the prey item relative to the video frame, as described elsewhere (Løw 2006, Steen 2004, Steen 2010). The body mass of birds has a relatively small intra-specific variation; a mean value for each prey species was therefore obtained from data most pertinent to the breeding season in Fennoscandia (Cramp and Simmons 1980, 1983, Cramp 1985, 1988, 1992, Cramp and Perrins 1993, 1994a,b, Matthysen 1998, Selås 2001). If an avian prey was identified to genus only, as for instance many thrushes (*Turdus sp.*) were, we calculated an average body mass of the possible species alternatives. For passerines, juveniles were assigned the same body mass as adults, whereas for grouse and shorebirds, the body mass of juveniles was estimated from shape and relative size on the video frame. The body mass of insects was obtained from Itämes and Korpimäki (1987). All insects recorded were assigned a body mass of 0.2 g since they were of similar size. The mass of unidentified bird remains was set to 15% of the mean avian body mass. We were unable to estimate the body mass of frogs and wood lemmings from the video frame, and these were consequently estimated from specimen trapped in the study area during the kestrels´ nestling period in 2007-2009 (G. A. Sonerud, unpublished data). The mass of the few juvenile mountain hare remains were set to 15% of the mean body mass of juvenile mountain hares (Bray et al. 2002). The body mass of unidentified voles was set to the mean body mass of an average *Myodes* vole, *Microtus* vole and wood lemming. Correspondingly, the body mass of unidentified small mammals was set to the mean mass of an average shrew, *Myodes* vole, *Microtus* vole and wood lemming. The body mass of unidentified prey was set to the mean body mass of all identified prey. The mass of unidentified prey remains was set to 15% of the mean unidentified prey mass. In some few cases only the rear part of the prey item was delivered. In these cases we set the mass to 75% of the estimated body mass of the given prey type.Estimated prey body mass of the different prey types (table 1) were used for the whole data set (2003, 2005, and 2006-2009).

Statistics

The rate of prey mass (g per h) delivered at kestrel nest p (G_p) was calculated by means of the equation

$$\mathrm{G_p} = \frac{1}{f_p}\sum_{i=1}^{n_p} k_{i,p} \qquad (1)$$

where p = 1, …, 55 denotes kestrel nest p, i_p = 1, … n_p denotes prey item i delivered at nest *p*, n_p denotes number of prey items delivered at nest *p* during the video monitoring period; $k_{i,p}$ denotes estimated mass (g) of prey item i_p, and f_p denotes the duration (h) of the video monitoring period at nest *p*.

We assume that the rate of prey mass delivered reflected consumption rate, because the mass-specific energy content and also the assimilation quotient (i.e. assimilated portion of the energy consumed) is quite similar for the different prey types (table 1).

To estimate the number of prey items of type j (i.e. insect, lizard, shrew, vole or bird) required to be delivered per hour to feed an average kestrel brood (i.e. 4.3 nestlings, see below) in our study we used the equation

$$N_j = \frac{G_{est}}{m_i} \qquad (2)$$

where G_{est} denotes estimated prey consumption (g^{-h}) calculated from the parameter estimates of the best fitted model with brood size fixed at 4.3, and m_j is the estimated body mass of item of prey type j.

Statistical analyses were performed with the software R, version 2.11.1 (R Development Core Team 2010), using analysis of variance and linear mixed effect model in the lme package (Pinheiro and Bates 2000). We used a linear mixed-effect model with prey mass delivery rate (G_p; g^{-h}) as the response variable, and brood size and average nestling age as the explanatory variables. We believe that the effect of age would be minor because the variation of nestling age in our data set was low, however we include it to control for a possible effect. Prey mass delivery rate, nestling age and brood size were $\log_{10}$ transformed. Year was included as a random factor to control for a possible variation associated with inter-annual changes in environmental conditions that may have influenced the delivery rate. When voles are rare and constitute a low proportion of the diet, the brood size of kestrels will normally be small (Korpimäki 1986, Korpimäki and Wiehn 1998, Wiebe et al. 1998). One may argue that any effect of brood size on prey delivery rate would be an artefact of kestrels having smaller broods when voles are rare and constitute a smaller proportion of the diet (Korpimäki 1986, Korpimäki and Wiehn 1998, Wiebe et al. 1998). Hence, prey mass delivery rate may not only be affected by brood size itself, but also by the associated proportion of voles in the diet. We therefore included the proportion of mass delivered made up by voles for each nest as a co-factor. The proportion of voles was $\log_{10}$ transformed, but this proportion was zero in five cases and we added a minimum value (i.e. lowest proportion value for this variable) to all before transforming. We used the most parsimonious model, and an explanatory variable was included only when the value of AIC_C (corrected Akaike Information Criterion) improved with ≥ 2.0 (Burnham 2002). We used AIC_C because it provides a better model selection than AIC for moderate sample sizes (Hurvich and Tsai 1991). From our best fitted model we used the parameter estimates to calculate the regression line between brood size and rate of prey mass delivered, $Y = \beta_0 + \beta x$, from which we used the slope β to estimate the effect of brood size on the rate of prey mass delivered. If the rate of prey mass delivered increases slower than the increase in brood size, i.e. if the slope is significantly smaller than one, each nestlings in larger broods will obtain less food compared to smaller broods. Finally, we used the parameter estimates to calculate prey mass consumption by the nestlings in an average brood. To control for contributions of the random effect, the values of $\beta_0 + \beta x$ and the associated 95% confidence intervals were calculated from the lme parameter estimates, using the function “intervals” in R (R Development Core Team 2010).

Results

The kestrels were recorded to deliver a total of 2282 prey items during the 2337 h of video monitoring at the 55 nests. The percentage of total number of items delivered was 0.4 for frogs, 2.9 for insects, 9.4 for lizards, 13.7 for birds, 12.4 for shrews, 60.0 for voles (19.2 for *Myodes* voles, 32.0 for *Microtus* voles, 2.4 for wood lemmings, and 6.5 for unidentified voles), 0.5 for unidentified small mammals, 0.04 for unidentified prey, 0.1 for bird remains, 0.1 for hare remains, and 0.4 for unidentified prey remains. In total, the kestrels were estimated to deliver 43283 g of prey during the filming. When using the estimated body mass of each prey type instead of prey numbers, the percentage of total prey mass delivered was 0.4 for frogs, 0.03 for insects, 2.6 for lizards, 24.7 for birds, 6.3 for shrews, 65.1 for voles (16.5 for *Myodes* voles, 38.5 for *Microtus* voles, 3.0 for wood lemmings, and 7.2 for unidentified voles), 0.5 for unidentified small mammals, 0.04 for unidentified prey, 0.04 for bird remains, 0.4 for hare remains, and 0.5 for unidentified prey remains.

The rate of prey mass delivery (G_p) was significantly affected by brood size (F_{48}= 24.39, $p < 0.001$, n = 55), which gave the best fit *(*AIC_C = -71.1). Adding the proportion of prey mass made up by voles gave a poorer fit (AIC_C = -68.5), as did adding nestling age (AIC_C =-64.5). For an average brood size (4.3), the parents were estimated to deliver 18.1 g^{-h} when applying the parameter estimates from the best fitted lme model. As a result, given the average brood size in our study, each nestling was estimated to consume on average 4.2 g^{-h}.

The earliest and latest recorded prey deliveries during the day at the kestrel nests occurred at 2.49 am and 11.39 pm, respectively. The maximum daily activity period was thus 20 hours 50 minutes. Based on the earliest and latest prey deliveries each day at the nests monitored continuously for 24 hours per day (estimate based on 88 nights and 96 mornings), the earliest prey delivery was on average at 5.34 am (±12.6 min) and the latest at 9.40 pm (±7.2 min). Hence, the daily activity period was on average 16 hours 6 minutes. Given a maximum daily activity period of 20.84 h, the daily delivery rate per nestling was 87.8 g^{-d} when applying the parameter estimates of the best fitted lme model. Correspondingly, given an average daily activity period of 16.10 h, the daily delivery rate per nestling was 67.8 g^{-d}.

The slope of the log-log plot of prey mass delivery rate as a function of brood size (Fig. 1a) was significantly less than one ($y = 0.98 + x*0.44$ (95% CI = 0.26-0.62). Hence, each nestling obtained less food with increasing brood size. For instance, a brood of two nestlings was estimated to consume a total of 12.9 g^{-h}, compared to 22.5 g^{-h} for a brood of seven. Thus, each nestling obtained 6.4 and 3.2 g^{-h} in a brood of two and seven, respectively.

The estimated number of prey items (N_j) required per hour to feed an average kestrel brood in our study (4.3 nestlings) was 90.55 when the diet was based solely on insects, and 3.42, 1.89, 0.83 and 0.52 when based solely on lizards, shrews, voles, and birds. This corresponds to one prey delivery per 40 sec if the diet was based solely on insects, and one delivery per 18, 32, 75 and 120 min if based solely on lizards, shrews, voles and birds, respectively.

Discussion

Of the 2282 prey items recorded delivered by the kestrels to their nests during our six years of study, voles were by far the most abundant prey both by number and mass, followed by birds, shrews and lizards, respectively. Insects and frogs were rarely taken as prey by the kestrels. The dominance of voles among prey taken by kestrels during the breeding period agrees with earlier findings (Village 1990, Korpimäki 1986). The mass-specific energy content of insects, frogs, lizards, shrews, voles and birds appeared to be quite similar, and this seemed to also be the case for the assimilated proportion of the energy content of the prey consumed (see references above). Hence, we assumed that the delivery rate of prey mass adequately reflected consumption rate.

With an average daily activity period of 16.10 h, each nestling was estimated to consume 67.8 g^{-d}. In comparison, Masman et al. (1989) found that nestlings which were hand-raised in the laboratory had an average food intake of 66.8 g^{-d} (seven nestlings 6-7 days old), compared to 62.6 g^{-d} for nestlings in the field in an average brood of 5.5 nestlings. (The average brood size was not given by Masman et al. (1989), and we therefore estimated it from the information given in their paper.) Geng et al. (2009) estimated the prey consumption of a kestrel nestling in the field to be 48.2 g^{-d} at an average brood of 4.8 nestlings. Our estimates were only 8% higher than the field estimates from Masman et al. 1989), but 29 % higher than the estimates from Geng et al. (2009). The daily activity periods of kestrels did not vary much between the different studies (16.1 h in ours vs. c. 17 h in that of Masman et al. (1989) and c. 15 h in that of Geng et al. (2009)). Hence, the discrepancy in daily consumption rate may be caused by other factors, for instance that our broods were on average smaller. In broods experimentally reduced by two nestlings, each nestling was found to consume 81 g^{-d}, compared to 61 g^{-d} in control broods (Dijkstra et al. 1990). To compare our estimate with that of Masman et al. (1989) and that of Geng et al. (2009) we set the activity period to 17 h and the brood size to 5.5, and the activity period to 15 h and the brood size to 4.8, respectively. This gave estimates of 62.4 and 59.4 g^{-d} per nestling, respectively, which is still slightly higher than the estimates of Masman et al. (1989), and markedly higher than the estimate of Geng et al. (2009). The difference may be due to our study area being situated further north and thus in a colder climate than the study areas of Masman et al. (1989) and Geng et al. (2009). A nestling´s food demand may be higher when the energy spent on thermoregulation is higher (Gil-Delgado et al. 1995 and references therein). The discrepancy may also have been caused by methodological differences. For records of prey deliveries, close-up video monitoring may be more accurate than observations from a hide and pellet analyses (Lewis et al. 2004). Masman et al. (1989) used direct observations close behind the nest box, and Geng et al. (2009) mainly used pellets from the nest box, although some data were obtained by direct observations from a hide.

We found that although prey mass delivery rate increased with brood size, each nestling obtained less food in larger broods. Hence, rearing a larger brood implied a cost for the individual nestling, although less energy may have been needed for thermoregulation in large than in small broods. However, because brood size may be confounded with prey availability (Korpimäki 1986, Korpimäki and Wiehn 1998, Wiebe et al. 1998), i.e. parents may be able to provide more prey and thus be able to raise a larger brood in years with high prey abundance, we are unable to conclude whether the increase in delivery rate with brood size was due to brood size in itself or due to higher vole abundance. However, the fact that the proportion of voles of the total prey mass delivered did not improve the model explaining delivery rate lends its support to a direct link between brood size and delivery rate. In a field experiment on kestrels, parents delivered more prey mass to enlarged broods, showing that to some extent they were able to compensate for larger broods by increasing hunting effort and prey delivery (Dijkstra et al. 1990). However, as in our study, each nestling consumed less food in large than in small (experimentally reduced) broods (Dijkstra et al. 1990). Less food obtained by each nestling in larger broods may cause lower nestling condition, as found in kestrels when brood size was manipulated (Dijkstra et al. 1990, Korpimäki and Rita 1996), which in turn may lead to lower survival (Korpimäki and Rita 1996 and references therein). On the other hand, smaller broods (e.g. 1-3 nestlings) may receive more food than is optimal for the parents´ total reproductive output. Data on juvenile survival and recruitment from our study area would be essential in revealing whether individual kestrel parents have an optimal brood size, and how this brood size might change with variation in the abundances of the various prey types.

During the first half of the nestling period, when the kestrel male usually provides most of the prey and the female feeds the nestlings (Village 1990, Sonerud et al. 2010), the male may be less able than the female to judge nestlings´ hunger (cf. Eldegard and Sonerud 2009, 2010). In some instances we observed prey provided by the male to be removed by the female just after she had finished a feeding session, indicating that the female is more able to sense when the nestlings are satisfied. Later in the season, when also the female may hunt, and as the nestlings become able to feed unassisted, the male more often delivers the prey directly to the nestlings (Village 1990, Sonerud et al. 2010). In this period, the male may be better able to judge the nestlings´ hunger and adjust his parental effort accordingly. In our study the largest brood size monitored was seven, which is similar to that found in other studies (Village 1990). From our parameter estimates (lme model), each nestling in a brood size of seven would obtain 3.2 g^{-h} (i.e. 51.2 g^{-d} for a 16.1 h day), which may be the lower threshold for what is optimal for the kestrel. In line with this, Kirkwood (1981) found the lowest consumption rate in hand-reared individual nestlings to be 59 g^{-d}. When less prey are available, parents may distribute the food selectively among the nestlings, favouring senior nestlings that may have higher reproductive value than juniors (Morris 1987).

The estimated delivery rate of insects required to feed an average kestrel brood in our study was one every 40 s, which is a rate unlikely to be achieved in the boreal forest. The corresponding estimate for lizards was one item every 18 min. Lizards probably occur too infrequently in our study area, due to our relative cold climate, , to be the sole prey of the kestrels (Pilorge 1987, Uller and Olsson 2003). In fact, lizards seem to be preyed upon by the kestrels in our area whenever available, determined by solar height and ambient temperatures (Steen et al. 2010c). If the kestrels were to feed solely on shrews or voles, they would have to deliver one prey item at the nest every 32 min or 75 min, respectively. The rate for voles seems realistic to attain when voles are abundant. However, for a diet to be based solely on shrews, shrews would have to be twice as abundant as voles in a vole peak years, which never occur in Fennoscandian boreal forests (e.g. Sonerud 1988, G. A. Sonerud, unpubl. data). Finally, if the kestrels were to feed on birds only, as may be the case in years with few shrews and voles (cf. Sonerud 1988), and on days with low ambient temperatures making lizards unavailable, they would have to deliver one prey every other hour. For raptors, birds are more difficult to catch than small mammals (Temeles 1985), and avian prey have to be plucked before being delivered at the nest (Village 1990, Løw 2006). Thus, kestrels in the Fennoscandian boreal forest would be unable to raise an average brood solely on insects or lizards, unlikely to do so solely on shrews or avian prey, but able to do so solely on voles in a vole peak year. This would explain why kestrels produce smaller clutches in years with few voles, as recorded in several studies (e.g. Korpimäki 1986, Korpimäki and Wiehn 1998, Wiebe et al. 1998).

In conclusion, in our Norwegian population of kestrels, the food demand of an average brood of 4.3 nestlings was about one vole per hour. This delivery rate would be realistic to achieve for a kestrel pair in peak vole years. In such years, the kestrels may respond by laying more eggs, although even in such favourable years, the optimal brood size may be restricted by the reduction in prey mass received by individual nestling.

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Table 1. Estimated body mass, mass-specific gross energy content (GE), and metabolizable energy (MEC) of prey types delivered at the kestrel nests. GE and MEC were obtained from Karasov (1990) and Studier and Sevick (1992) for insects, from Tryjanowski and Hromada (2005) and Voituron et al. (2002) for lizards, and from Masman et al. (1986) for shrews, voles and birds.

Prey type	Body mass (g)	GE (kJ/g)	MEC
Insect*	0.2	24.5	0.77
Common lizard	5.3±0.3 (n=54)	22.1	0.75
Frog**	22.6±4.0 (n=7)	—	—
Shrew	9.5±0.3 (n=64)	21.6	0.65
Myodes sp.	16.7±1.5 (n=28)	21.5	0.70
Microtus sp.	22.9±1.8 (n=21)	21.5	0.70
Wood lemming**	25.2±0.9 (n=100)	21.5	0.70
Vole indet.***	21.8	21.5	0.70
Small mammal indet***	16.6	—	—
Mountain hare part*	60.0	—	—
Bird	34.7±2.5 (n=118)	22.3	0.75
Bird remain***	5.2	—	—
Prey indet.***	17.2	—	—
Prey remain indet.***	2.6	—	—

*Estimated from the literature (see text).

**Estimated from specimen snap-trapped during the kestrels´ nestling period in 2007-2009.

*** Average estimated mass of recorded prey (see text).

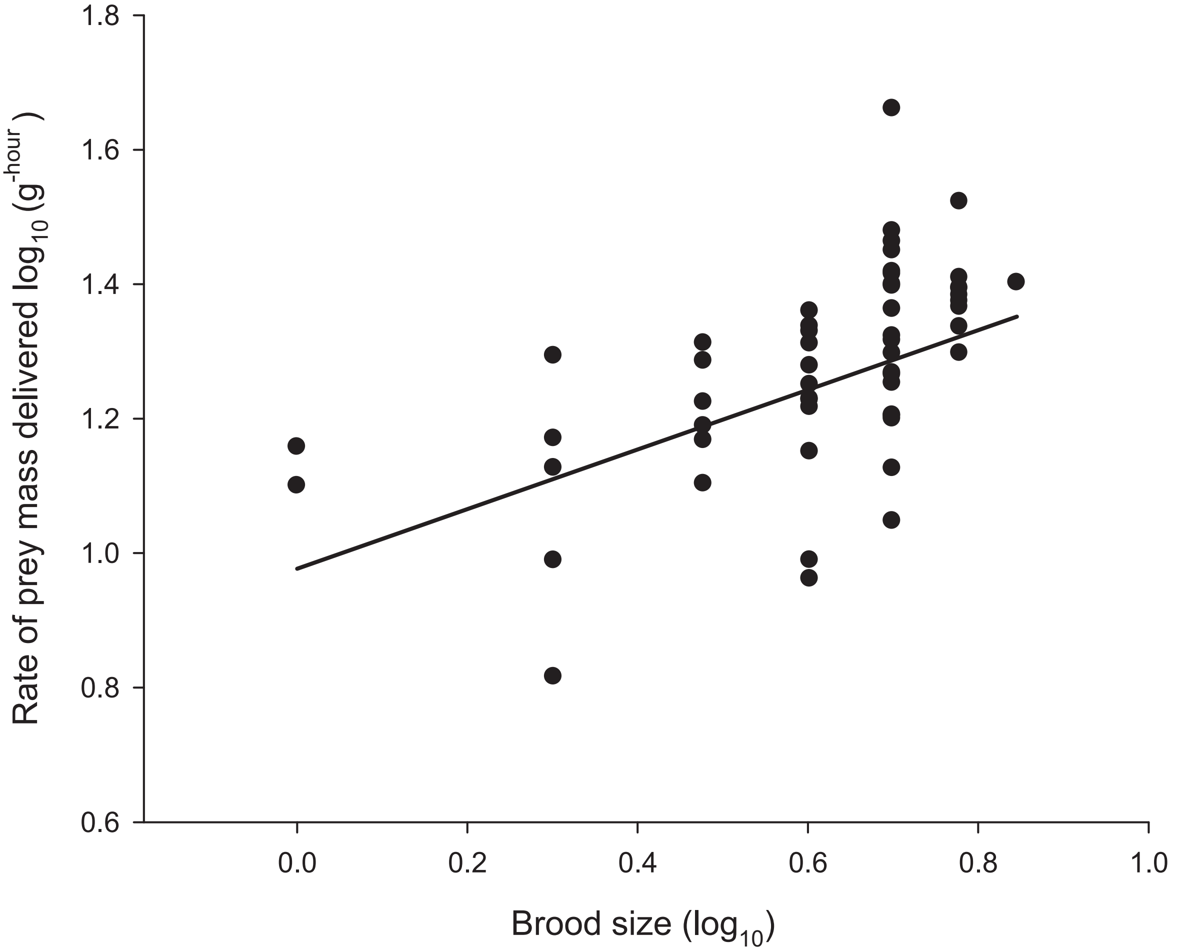

Figure 1. Prey mass delivery rate (g^{-h}, $\log_{10}$ transformed) for kestrel nests regressed on brood size (g^{-h}, $\log_{10}$ transformed). The regression line is calculated from the parameter estimates of lme model ($y = 0.98 + x*0.44$, $F = 24.4$, $df = 48$ $p<0.001$, $n=55$ nests, random effect = 6 years).

Paper VI

Parents adjust feeding effort in relation to nestling age in the Eurasian kestrel (*Falco tinnunculus*)

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Abstract

In altricial birds, parental food provisioning is essential for successful growth and development of the offspring, and parents are assumed to maximise the total food delivery to the brood given the time constraints set by self-feeding and food collecting. Older nestlings may require more food than younger ones, and nestlings may need more energy when growth rate is higher. We examined whether parents of the European kestrels (*Falco tinnunculus*) adjusted their feeding effort in relation to the age of the nestlings by video monitoring prey deliveries in ten nests during one breeding season. The daily rate of prey mass delivered by the kestrels was strongly associated with nestling age, with a maximum occurring when the nestlings were 16.7 days. This was close to the predicted age of 15.2 days when the growth of the nestlings settled down. The change in daily rate of prey mass delivered was mostly an effect of a corresponding change in the daily number of prey items delivered, but also a change in the size of prey delivered. This indicates that the kestrels adjusted the parental effort in relation to the changing needs of the young. The trend of decreasing prey size with increasing nestling age found in the kestrel is opposite to that found in other altricial birds, and may be unique to raptors due to their ability to dismember large prey for young nestlings.

Keywords: Eurasian kestrel, *Falco tinnunculus,* feeding effort, nestling age, prey delivery rate, prey mass

Introduction

Parental food provisioning in altricial birds is essential for successful growth and development of the offspring, and parents are assumed to maximize the total food delivery to the brood given the time constraints set by self-feeding and food collecting (Ydenberg 2007). Selection will favour parents to capture and provide prey that most optimally covers the daily energy need by the offspring (Fagerström et al. 1983 and references therein) with a minimum cost to the parents (Trivers 1974). Older nestlings are larger and may require more food than younger ones. However, growth rate is not constant, and nestlings may need more energy growth rate is higher (Barba et al. 2009). Parental food provisioning increases in general with nestling age, especially during the phase when the nestlings' growth rate is at its peak. When the nestlings approach their final body mass the provisioning rate tends to level out (e.g. Grundel 1987, Blondel et al. 1991, Barba et al. 2009). There is also a tendency for prey size to increase with nestling age because the restricted swallowing capacity of the nestlings improves as they grow (Slagsvold and Wiebe 2007).

An excellent species to investigate for relationships between parental effort and nestling age is the well-studied Eurasian kestrel (*Falco tinnunculus*), hereafter called the kestrel. This species lives in open landscapes and feeds mainly on ground dwelling animals like voles (Cricetidae), shrews (Soricidae) and lizards, and also on birds and insects (Village 1990). Kestrels respond both numerically and functionally to voles; kestrels raise fewer offspring and feed on a wider variety of prey, including more birds, lizards and insects during years with low vole abundance (Korpimäki and Norrdahl 1991, Fargallo et al. 2003). Kestrel parents appear to adjust their feeding effort to the current needs of the young (Daan et al. 1989). We studied this relationship in more detail by video monitoring kestrel nests, which enabled us to obtain more precise measurements of prey mass delivered by the parents than traditional analyses based on pellet samples or direct observation from a hide would have done (Lewis et al. 2004). We examined whether parents of the European kestrels (*Falco tinnunculus*) adjusted their feeding effort in relation to the stage of the breeding season, viz. by increasing the rate of prey mass delivered with increasing nestling age. Masman et al. (1989) found that food intake in laboratory-raised kestrel nestlings increased from day 11 to day 18 after hatching followed by a decrease over the remaining nestling period until day 30. A non-linear relationship would be expected, because above a certain age the nestlings would grow at a gradually slower rate (e.g. Grundel 1987, Blondel et al. 1991, Barba et al. 2009). To predict the age at which the growth pattern changes from accelerating to decelerating we analysed data from Village (1990, Fig. 54) on body mass of kestrel nestlings. From the growth curve we calculated the inflection point and the point of upper maximum curvature (Fig. 1). The inflection point denotes the time when the growth is at the maximum (i.e. for a sigmoid curve, the time when growth is half complete). We did not expect a peak in the energy need of the nestlings at this point because the nestlings are still growing fast, and because larger nestlings that have passed the peak of growth and are growing slower may still need more food than smaller nestlings that are at the peak of growth. Therefore, we needed to adjust for changes in nestling body mass during growth. More precisely, we needed to locate the point where the growth rate no longer continues to rapidly rise and instead follows either a stable state or slow rise (cf. Stirling and Zakynthinaki 2008), also termed the upper maximum curvature (UPMC), i.e. the point of maximum deceleration (Banks 1994). Using the data on nestling growth in Village (1990) and following Banks (1994) we found that the UPMC is reached when nestlings are 15.2 d old. Nestlings need to allocate energy not only for growth in general, but also for growth of muscles and feathers (Kirkwood 1981), which develop after the kestrel nestlings have attained their overall maximum mass (Kirkwood 1981). Hence, the body mass of the nestlings may in itself not be a sufficient index for energy demand. To account for this we analysed data from Kirkwood (1981, fig. 9.15) on the metabolisable energy (ME) intake of kestrel nestlings. We generated a smoothed curve to visualise the peak in ME intake approached by the nestlings at an age of c. 15-17 d (Fig. 2). We predicted that the rate of prey mass delivered by the parents would peak when the nestling age was close to the point of UPMC, but with a small time lag due to the peak in ME intake (Kirkwood 1981).

The video filming enabled us not only to test whether parents adjusted the delivery rate of prey mass to nestling age, but also whether they adjusted prey size. Therefore, we also analysed at which nestling age the delivery rate of prey items peaked, and whether prey size changed with nestling age. In the early nestling period, the female kestrel is permanently present at the nest, and receives prey from the male to feed it to the young (Village 1990). After about two to three weeks, the nestlings start to feed unassisted and the female starts to hunt (Village 1990). We would expect males to provide larger prey when the female is at the nest, because larger prey items are more efficient to ingest when the female feeds the nestlings (Steen et al. 2010a). As nestlings become able to feed unassisted, we would expect smaller prey items like insects, lizards and shrews to be delivered more often, because the nestlings would be able to feed unassisted on such small prey items earlier (R. Steen et al. unpublished data). This would relieve the female from feeding the nestlings sooner and allow her to start hunting (Sonerud et al. 2010). Hence, we predicted that prey size would decline with nestling age. Note that this is opposite to the prediction based on the hypothesis that male and female raptors have different feeding niches (e.g. Selander 1966, Snyder and Wiley 1976, Newton 1979, Andersson and Norberg 1981, Temeles 1985), because if they we would expect that the mean prey size delivered to the young would increase after the larger female started hunting.

Methods

Video monitoring

The estimates of the daily rate of prey mass consumption by a nestling were based upon video monitoring of adult kestrels delivering prey at ten nests in the boreal and hemi-boreal zones in Hedmark county in south-eastern Norway (61° N, 12° E) during June-July in 2007. The nests had a mean nearest neighbour distance of 3.3 ± 0.3 (range 2.3-5.8) km, and were in nest boxes situated 637 ±15 (range 558-694) m a.s.l. The study area is dominated by large bogs and intensively managed coniferous forest with a high proportion of clear-cuts, and with only negligible patches of farmland. One week or more after hatching the ten original nest boxes were replaced with nest boxes designed specifically for filming. A CCD camera was placed in the top back corner of the nest box and pointed towards the entrance of the nest box. The camera was mounted with a wide angle lens to cover a broad view inside the nest box, connected with a video cable to a mini digital video recorder (mini DVR) which stored data on SD cards. For details of video equipment, see Steen (2009). The average age of the last hatched nestling was 10.2 ± 0.6 days (range 8-12) when filming started and 26.7 ± 0.5 days (range 24-29) when it ended. Average brood size was 5.0 ± 0.3 (range 3-6). No nestlings died during filming; i.e. brood size in each nest was constant. The monitoring of each nest started on different days; one nest at the first day (age of the last hatched nestling was 12 days), one nest at the second day (age of the last hatched nestling was 12 days), one nest at the third day (age of the last hatched nestling was 12 days), three nests at the fourth day (ages of the last hatched nestling were 8, 9 and 9 days, respectively), three nests at the fifth day (ages of the last hatched nestling were 12, 8 and 8 days, respectively) and finally one nest at the sixth day (age of the last hatched nestling was 12 days).

From the video recordings we identified each prey item delivered by the parents to main type, i. e. whether it was a lizard, shrew, vole, bird, or a fragment of a bird or of an unidentified prey item. To estimate the mass of each of the prey types we used the estimates of prey body mass data provided in (Steen et al. 2010b), which were based on estimates of the body mass of single prey items delivered to 19 kestrel nests in our study area in 2003 and 2005. In case of the kestrel being prey-size selective when hunting small mammals, as shown by Masman et al. (1986), our estimates are more reliable than mean values obtained solely from the literature.

Prey mass delivered

We estimated the daily rate of prey mass delivered to each nest during the nestling phase. The measurements started on the first complete day of monitoring after the onset of filming (i.e. immediately after midnight) and ended on the last complete day of monitoring before conclusion of filming (i.e. immediately before midnight). Due to technical failure during monitoring, two days of recording were subtracted for two nests and one day for a third nest. The total prey mass (g) delivered per nestling at each nest for each day (G) was calculated by means of the equation

$$\mathrm{G} = \frac{1}{b}\sum_{i=1}^{n} k_i \qquad (1)$$

where $i = 1, \ldots, n$ denotes prey item i delivered during the day, k_i denotes estimated body mass (g) of prey item i, and b denotes brood size. We calculated a value of G for each of the 151 complete days of monitoring.

Statistics

To calculate the growth curve of the kestrel nestlings, we extracted the mean values from the growth curve presented in Village (1990, figure 54). We used a non-linear regression in the Sigma-Plot version 9.01 graphic package (SPSS Inc.) to obtain a sigmoid (i.e. three-parameter nonlinear regression) growth curve by means of the equation

$$f(x) = \frac{a}{1 + e^{-\left(\frac{x - x_0}{b}\right)}} \qquad (2)$$

where $f(x)$ denotes the nestling body mass (g), a denotes the upper asymptote, x denotes nestling age (d), x_0 denotes the nestling age when $f(x)$ is 50% of the maximum, and b denotes the slope at x_0.

We used the second derivative to find the inflection point of the curve ($f(x)'' = 0$), where the growth rate peaks, and the third derivative to find the upper point of maximum curvature ($f(x)''' = 0$, where the growth flattens down (Banks 1994).

To calculate the ME intake of the kestrel nestlings, we extracted the mean values from the figure presented in Kirkwood (1981, Fig. 9.15). To visualize the peak we generated a smoothed curve by use of smooth data option in Sigma-Plot version 9.01 graphic package (SPSS Inc.)

Statistical analyses were performed with the software R, version 2.8.1 (R Development Core Team 2008). We used a linear mixed effect model (lme) in the nlme package (Pinheiro and Bates 2000), and tested if there was a change in the daily rate of prey mass delivered per nestling as a function of nestling age. Daily rate of prey mass delivered per nestling (G) was used as the response variable, and nestling age and brood size as explanatory variables.

Any changes in the daily rate of prey mass delivered per nestling as a function of nestling age may not only be an effect of parents adjusting their prey item delivery rate, but may also be an effect of parents providing smaller or larger prey items. To test for this we firstly used the number of prey items delivered per day per nestlings as the response variable, and nestling age as the explanatory variable. Secondly, we used the daily average body mass of prey items delivered as the response variable, and nestling age and brood size as the explanatory variables.

In addition, we tested whether a seasonal effect was present (e.g. prey availability), rather than nestling age, by using season as an explanatory variable (i.e. onset of first filming and days thereafter). Both nestling age and season are confounding factors that are associated with each other and most likely also the outcome. The variables age and season were therefore run separately in the models. For all the models we tested whether a linear (i.e. $f(x) = \beta_0 + \beta x$) or non-linear (i.e. $f(x) = \beta_0 + \beta_1 x + \beta_2 x^2$ or $f(x) = \beta_0 + \beta_1 x + \beta_2 x^2 + \beta_3 x^3$) relationship gave the best fit, the model with the lowest AIC-value was selected (Burnham and Anderson 1998). We kept to the model when the differences in AIC were larger than 2.0 between this and other models (Burnham 2002). Brood size was considered to be a co-factor and only included if AIC improved with 2.0 or more. Breeding pair was treated as a random factor to control for a possible variation caused by individual differences.

The values of the response variables; daily rate of prey mass delivered per nestling and number of prey items delivered per day per nestling, were $\log_{10}$ transformed to obtain approximately normal distributions. To control for contributions of the random effect the values of the intercept, the slope and the associated 95% confidence intervals were calculated from the lme parameter estimates, using the function "intervals" in R (R Development Core Team 2008). Mean and standard error is presented as mean ± SE.

Results

The parent kestrels delivered 3595 prey items during the monitoring period. Of these, lizards constituted 2.7 %, shrews 9.8 %, voles 60.2 %, unidentified small mammals (shrews or voles) 19.4 %, birds 4.0 %, 3.9% were unidentified prey items, and 0.3 % were fragments of a prey. The daily rate of prey mass delivered was highly associated with nestling age, and a non-linear relationship gave the best fit (table 1a, table 2 and Fig. 3). Removing $\beta^2 x$, adding βx^3, or adding brood size as a co-factor, both gave a poorer fit (table 1a). Nestling age gave a much better fit than by using season (ΔAIC = 71.4, ΔAIC = the difference in AIC-value between the model with age- and model with season as explanatory variable).

The nestling age at which the peak in daily rate of prey mass delivered per nestling occurred (the maximum of the positive "U-shaped" curve in Fig. 2) was found by setting the second derivative of the function given in fig. 2 to zero. This gave the value 16.7 d, which was close to the time when the growth "settled down" (UPMC), i.e. 15.2 d; Fig. 1 and 4), and even closer to the peak in ME intake (i.e. 15-17 d; Fig. 2). From the function given in Fig. 3, the maximum rate of prey mass delivered per nestling was estimated to be 105.5 g^{-d} when they were 16.7 d old, compared to 71.7 g^{-d} per nestling when the nestlings were 9 d old, and 48.4 g^{-d} when they were 28 d old (Fig. 3).

The daily rate of prey items delivered per nestling was highly associated with nestling age, and a non-linear relationship gave the best fit (table 1b, table 3 and Fig. 5). Removing $\beta^2 x$, adding βx^3, or adding brood size as a co-factor, both gave a poorer fit (table 1b). Nestling age as a factor gave a much better fit than by using season (ΔAIC = 57.9).

The peak in daily rate of prey item deliveries per nestling occurred when the nestlings were 17.7 days old, which was 1.0 day later than the peak in daily rate of prey mass delivered per nestling.

The daily average body mass of single prey items delivered decreased significantly with nestling age and a linear regression gave the best fit (table 1c and Fig. 6). Adding $\beta^2 x$, adding βx^3, or adding brood size as a co-factor, all gave a poorer fit (table 1c). However, nestling age gave approximately same fit as season (ΔAIC=-2.0), hence we cannot be conclusive of whether the decrease in average body mass is caused by nestling age or by a seasonal effect (e.g. change in prey availability).

Thus, the adjustment to nestling age of the daily rate of prey mass delivered per nestling was due to parents adjusting their prey item delivery rate, as well as parents adjusting prey size by providing smaller prey items as nestlings grew older.

Discussion

Of the 3595 recorded prey items delivered at the kestrel nests, voles were most abundant by number, which fits with earlier findings for the Eurasian kestrel (Korpimäki 1986, Village 1990, Korpimäki and Norrdahl 1991). The daily rate of prey mass delivered per nestling was highly associated with nestling age, and exhibited a typical positive “U-shaped” curve which peaked when the nestlings were 16.7 d old. This was very close to the estimated 15.2 d for the time when growth settled down (UPMC, i.e. maximum deceleration) and even closer to the peak in ME intake (15-17 days). This indicated that the parent kestrels adjusted their feeding effort to the stage of the breeding season (c.f. Johnsen et al. 1994). A similar pattern has been found for passerine birds (Grundel 1987, Blondel et al. 1991, Barba et al. 2009). The male may be less able than the female to judge the nestlings′ hunger during the first half of the nestling period (cf. Eldegard and Sonerud 2009, 2010), when he usually provides most of the prey through the female (Village 1990). Later on, the female also may hunt, and as the nestlings become able to feed unassisted, the male more often delivers the prey directly to them (Village 1990, Sonerud et al. 2010). Hence, later in the nestling period, the male may be better able to judge nestling hunger and adjust his hunting and feeding effort accordingly.

As expected there was a slight delay (1.5 days) between the predicted and the observed peak in prey mass delivery rate. This may have been caused by a peak in food demand actually occurring slightly later than the time when growth flattens down, e.g. due to continued growth of muscles and to rapid feather growth (Kirkwood 1981). Also, increased activity of the nestlings, including unassisted feeding and sibling competition, may have an effect on this (Village 1990). In kestrel nestlings, body mass peaks at 21-25 days, whereas the gut and liver are largest between 10-20 days, and then even larger than those of the adults (Kirkwood 1981). Thereafter, the pectoral muscle mass increases (Kirkwood 1981). The feathers are growing rapidly at the age of 15-20 days, and both down and feathers are still growing until 35-45 days after hatching (Kirkwood 1981). Hence, the body mass of the nestlings may in itself not be a sufficient index for energy demand (Kirkwood 1981), as energy required for growth of muscles and feathers needs to be accounted for.

We assume that the growth curve provided by Village (1990) is representative for the kestrels in our population, because other studies of nestling growth in wild kestrels in Europe have yielded similar results (Village 1990 and references therein). We also assume that the rate of prey mass delivered adequately reflects consumption rate. One may argue that the mass of a prey item is a biased measure of the energy gained from it, since the mass-specific energy content may vary between different prey types. However, the mass-specific energy contents of lizards, shrews, voles and birds are similar, as is also the assimilated proportion of the energy content of the prey consumed (see Steen et al. 2010b). Brood size did not contribute to the model, probably because the variation in brood size among the ten breeding pairs sampled was low.

The estimated maximum daily rate of prey mass delivered per nestling was 105.5 g^{-d} and was achieved when the nestlings were 16.7 days old, compared to 71.7 g^{-d} when they were 9 d and 48.4 g^{-d} when they were 28 d. Kirkwood (1981) recorded a maximum daily consumption of 90-120 g^{-d} for hand-raised individual kestrel nestlings, and on average each nestling consumed 59 g^{-d} . Masman et al. (1989) found a corresponding result of 66.8 g^{-d} for hand-raised nestlings in the laboratory and 62.6 g^{-d} per nestling in the field, while Geng et al. (2009) found this to be 48.2 g^{-d} per nestling in the field. Masman et al. (1989) conducted their experimental feeding when nestlings were 6-7 d old, which means that an estimate being 7.5 g^{-d} (10%) lower than ours for 9 d old nestlings compares well. The estimates from the field studies are more difficult to compare with ours, as they are averages for nestlings of varying in age.

The nestlings´ food demands peak at an age of 16-17 days, when the female often participates in the hunting (Village 1990, Fargallo et al. 2003). This enables the parents to deliver more prey items per day, and thus better match the nestlings´ food demands. By the time the nestlings were 23 d old, the parents had relaxed their delivery rate and provided a similar daily mass as when the nestlings were 12 d old. The adjustment of the daily rate of prey mass delivered was mostly an effect of parents adjusting their daily rate of prey items delivered, but also an effect of providing smaller prey items as the nestlings grew older.

However, we found that the change in average prey size may as well be explained by a seasonal effect, and we cannot be conclusive of whether the variation is caused by nestling age or seasonal variation. When kestrels provide smaller prey items like insects, lizards and shrews, their nestlings are able to feed unassisted earlier (R. Steen et al. unpublished data). The female is thus relieved from only feeding the nestlings and may start to hunt earlier (Sonerud et al. 2010). However, the parents then have to maintain a higher feeding rate and thus foraging effort, to meet the food demand of the nestlings than they would have to if they provided larger prey items. Therefore, as long as the male provides all prey alone he may be more likely to deliver larger items at a lower rate to maintain the mass required. Larger items are also more efficient to ingest than smaller ones as long as the nestlings are fed by the female (Steen et al. 2010a). When the nestlings are c. two weeks old the female also participates in the foraging (Village 1990, Fargallo et al. 2003), and the parents may then together achieve a higher delivery rate. They are thus more likely to meet the nestlings' food demand even with smaller prey items, which the nestlings are able to ingest unassisted. Hence, as the nestlings become older and their food demand declines, the parents become even more likely to meet this demand by delivering small prey. As a consequence, we would expect the kestrels to deliver smaller prey items as the nestlings grow older.

In conclusion, the daily rate of prey mass delivered by parent kestrels was highly associated with nestling age, and peaked only marginally later than the point where growth is "settling down" (UPMC, i.e. maximum deceleration) and matched the peak in nestlings ME intake. This indicates that the parents adjusted their feeding effort to the changing need of the nestlings. The daily rate of prey items delivered peaked somewhat later than that of prey mass delivered, because the daily average body mass of prey items delivered declined linearly with nestling age. The latter is opposite to what is found in passerine birds, where prey size increases with nestling age because the restricted swallowing capacity of the nestlings improves as they grow larger (Slagsvold and Wiebe 2007). The kestrel, as other raptors, is able to dismember large prey, and is therefore relieved from the prey-size constraint set by the limited swallowing capacity of young nestlings. However, when the nestlings start to feed unassisted, the constraint set by their dismembering skills and swallowing capacity would apply (cf. Steen et al. 2010c).

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Table 1. Model selection with a) the daily rate of prey mass delivered per nestling; b) daily rate of prey items delivered per nestling; c) the daily average body mass of prey delivered as response variable, and nestling age and brood size as explanatory variables. Where x denotes nestling age and where x_2 denotes brood size. ΔAIC = the difference in AIC-value between the best fitted model and model after adding or removing a variable. Therefore, the best model had a ΔAIC = 0.00.

Test	Model	AIC	ΔAIC
a)	$f(x) = \beta_0 + \beta_1 x + \beta_2 x^2$	-316.85	0
	$f(x) = \beta_0 + \beta x$	-259.81	57.04
	$f(x) = \beta_0 + \beta_1 x + \beta_2 x^2 + \beta_3 x^3$	-303.53	13.33
	$f(x) = \beta_0 + \beta_1 x_1 + \beta_2 x^2 + \beta x_2$	-309.12	7.73
b)	$f(x) = \beta_0 + \beta_1 x + \beta_2 x^2$	-305.23	0
	$f(x) = \beta_0 + \beta x$	-263.57	41.66
	$f(x) = \beta_0 + \beta_1 x + \beta_2 x^2 + \beta_3 x^3$	-286.91	18.32
	$f(x) = \beta_0 + \beta_1 x_1 + \beta_2 x^2 + \beta x_2$	-297.01	8.23
c)	$f(x) = \beta_0 + \beta)$	615.46	0
	$f(x) = \beta_0 + \beta_1 x + \beta_2 x^2$	623.46	8.00
	$f(x) = \beta_0 + \beta_1 x + \beta_2 x^2 + \beta_3 x^3$	632.04	16.57
	$. f(x) = \beta_0 + \beta_1 x_1 + \beta_2 x^2 + \beta x_2$	625.23	9.77

Table 2. Parameter estimates of the best- fitted model for the effect of nestling age on the daily rate of prey mass delivered per nestling by Eurasian kestrel parents (n = 151 days, 10 breeding pairs).

	Value	SE	df	t-value	p-value
Intercept	1.313	0.083	139	15.77	<0.001
Age	0.083	0.093	139	8.88	<0.001
Age^2	- 0.002	0.0003	139	-9.78	<0.001

Table 3. Parameter estimates of the best fitted model for the effect of nestling age on the number of prey items delivered per day per nestling by Eurasian kestrel parents (n = 151 days, 10 breeding pairs).

	Value	SE	df	t-value	p-value
Intercept	0.0166	0.087	139	0.19	0.8484
Age	0.079	0.010	139	8.13	<0.001
Age^2	- 0.002	0.0003	139	-8.45	<0.001

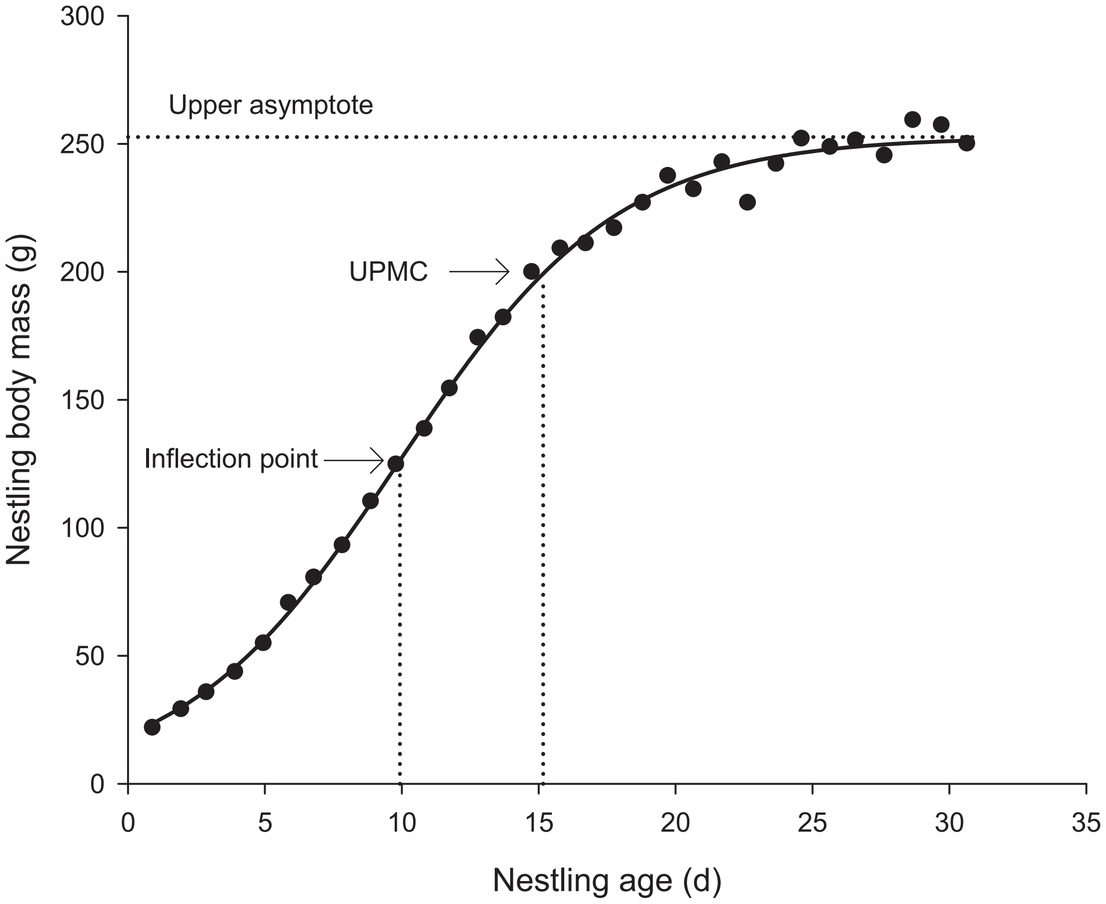

Figure 1. Growth curve of Eurasian kestrel nestlings extracted from Village (1990, Fig. 54). We calculated the inflection point (*f (x)* '' = 0), and the point of upper maximum curvature (*f (x)* ''' = 0, UPMC), at the point where growth is “settling down (i.e. maximum deceleration) (Banks 1994). ($f (x) = 252.63(1/(1+e^{-((x-9.94)/3.97)})$, $R^2 =0.99$, $p < 0.001$, $n = 30$).

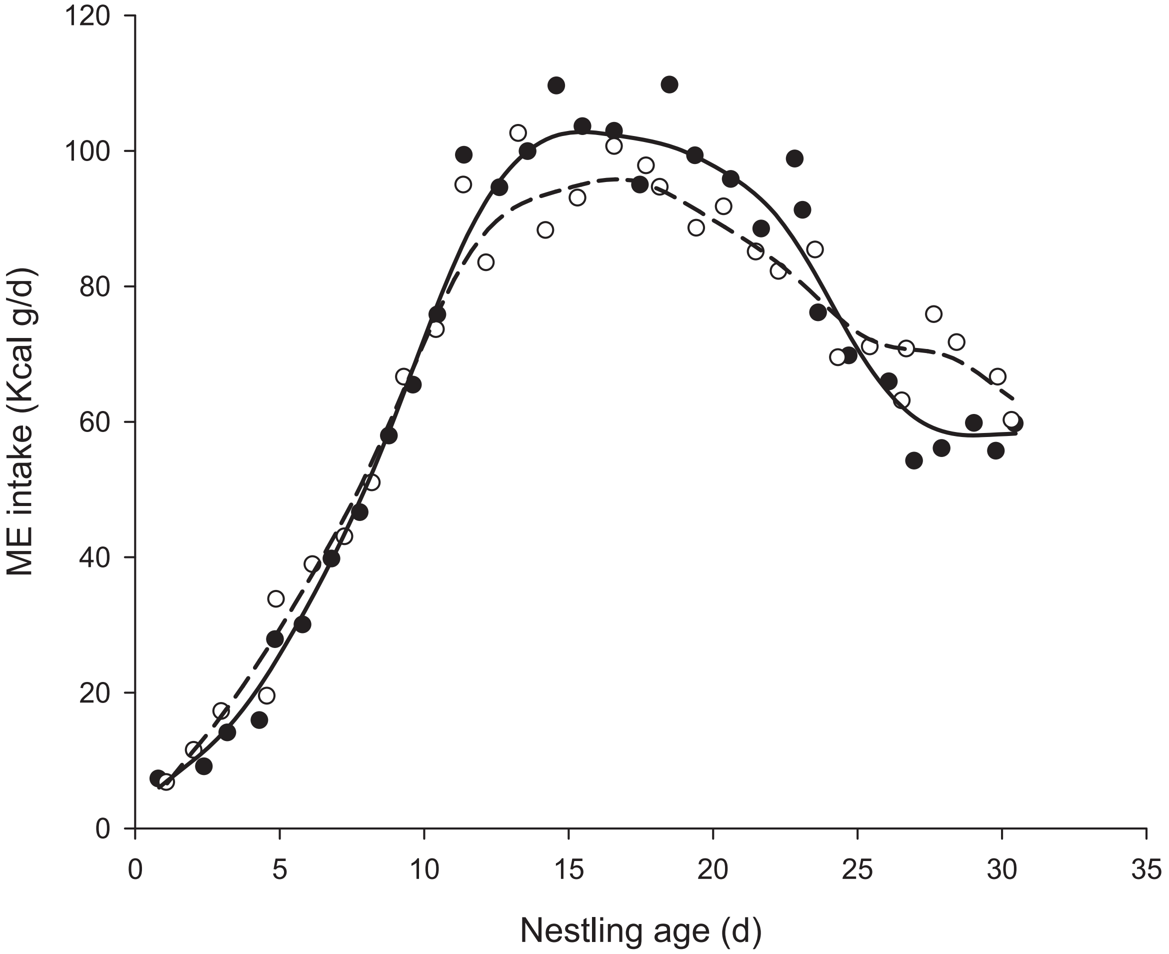

Figure 2. ME intake of Eurasian kestrel nestlings extracted from Kirkwood (1981, Fig. 9.15). To visualize the peak we generated two smoothed curves, nestlings on a mouse diet (filled circles, solid line) and nestlings on a mouse and one day old chick diet (open circles, dashed line).

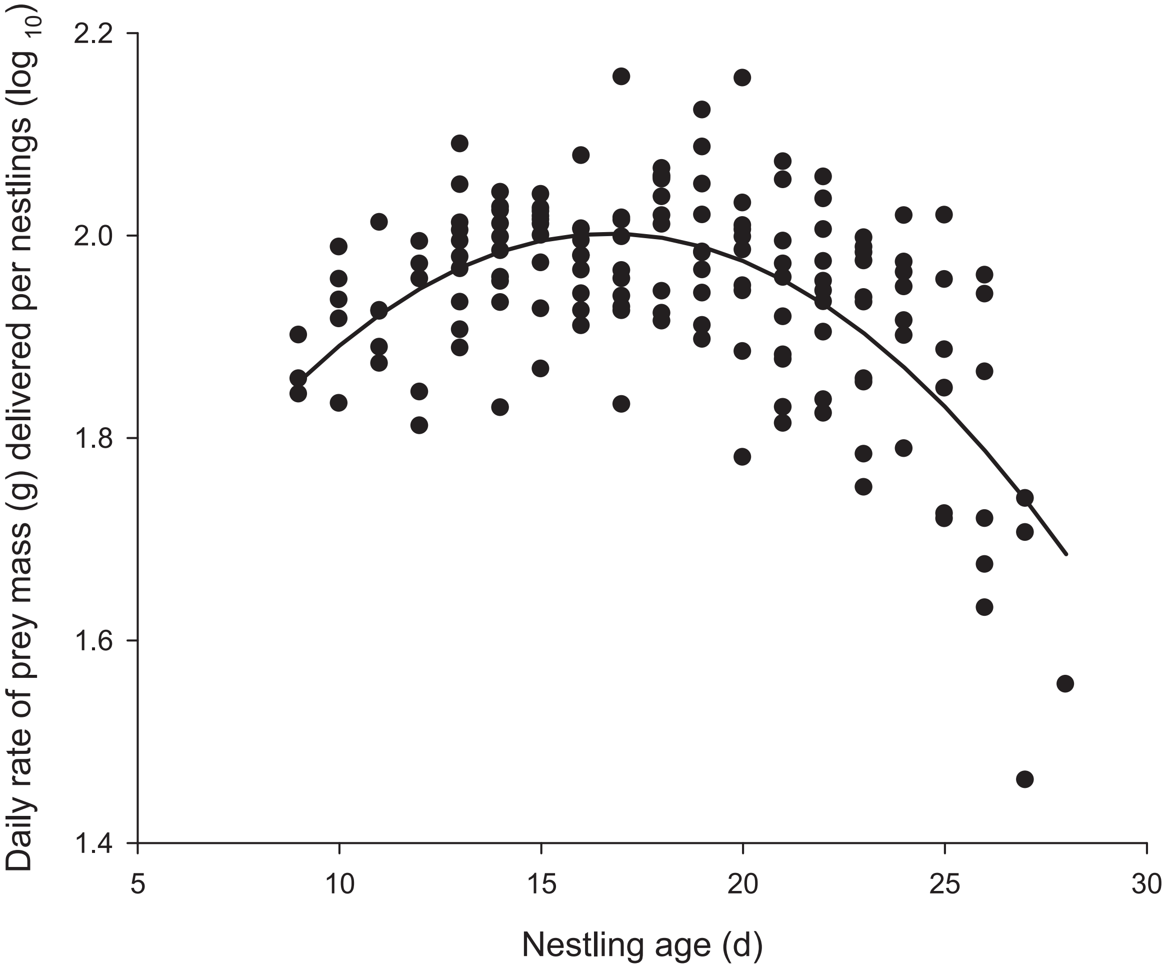

Figure 3. The daily rate of prey mass delivered per nestling by Eurasian kestrels in relation to nestling age. The regression is calculated from the parameter estimates of the best fitted lme model ($f(x)$ = 1.31 (CI=1.15-1.48) + 0.08 (CI=0.06-0.10) x – 0.002 (CI=-0.003-(-) 0.002) x^2)

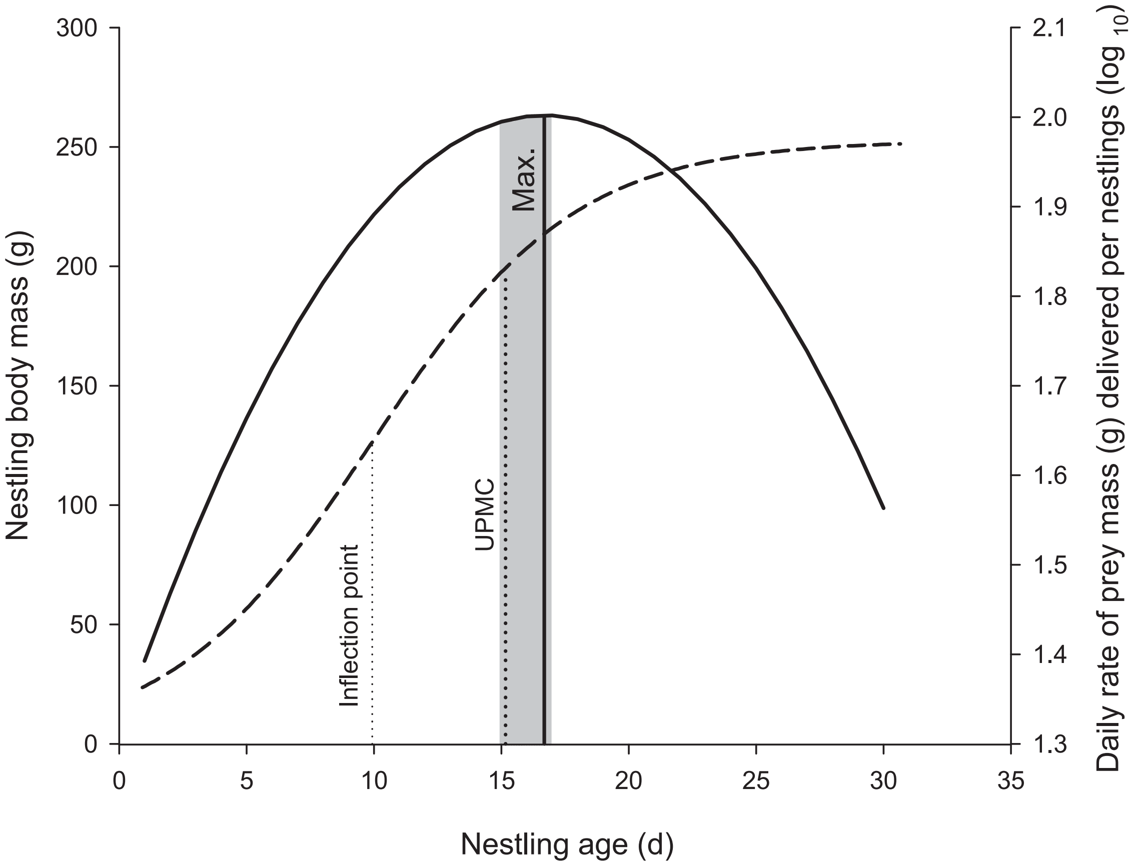

Figure 4. The estimated growth curve for Eurasian kestrels obtained from Village (1990) with the inflection point and upper maximum curvature (UPMC) shown, in comparison with our curve for the daily rate of prey mass delivered per nestling, with its inflection point (i.e. the estimated maximum daily rate of prey mass delivered by the parent per nestling) shown. The shaded area visualising the c. peak in ME intake (i.e. 15-17) from Kirkwood (1980).

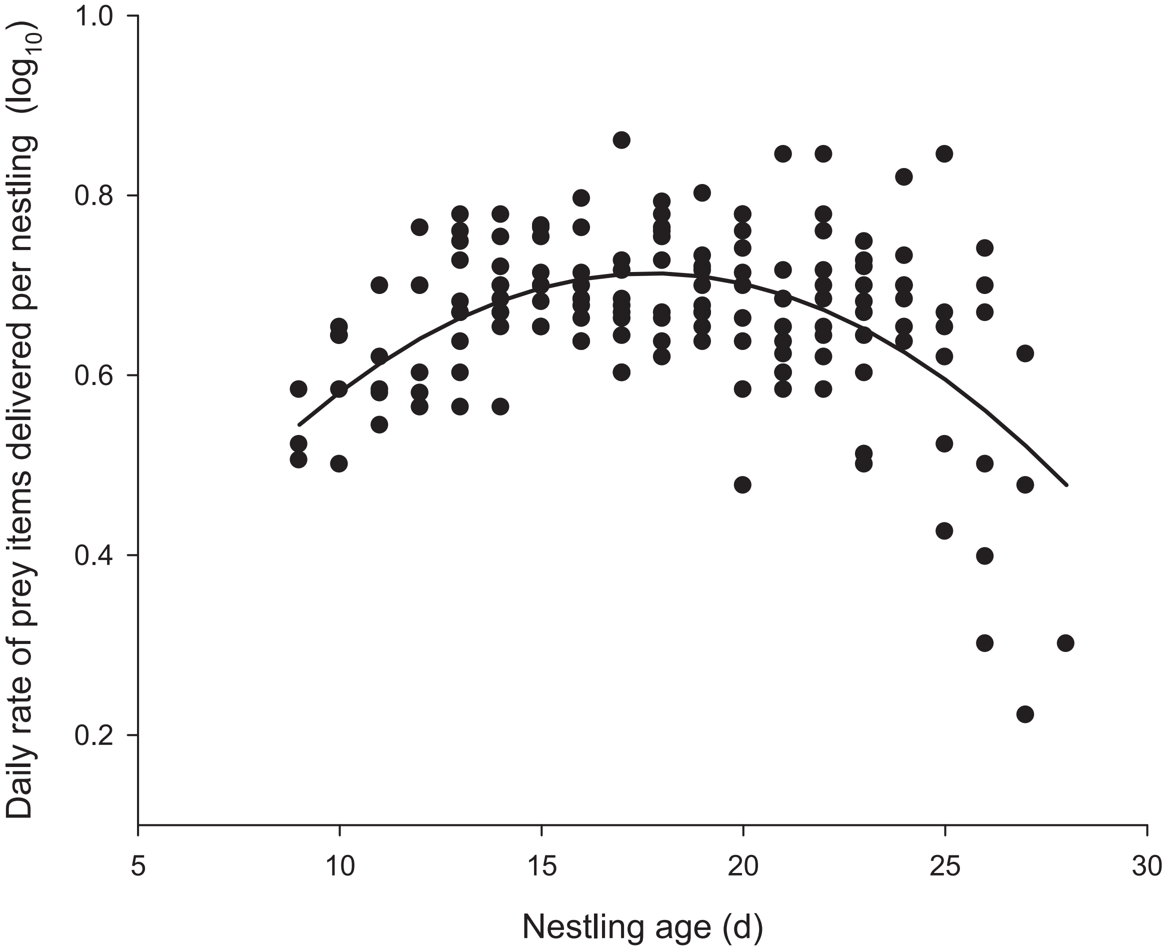

Figure 5. The number of prey items delivered per nestling per day by parent Eurasian kestrels in relation to nestling age. The regression is calculated from the parameter estimates of the best fitted lme model (*f (x)* = 0.017 (CI=-0.15-0.19) + 0.08 (CI=0.06-0.10) x – 0.002 (CI=-0.003-(-) 0.002) x^2).

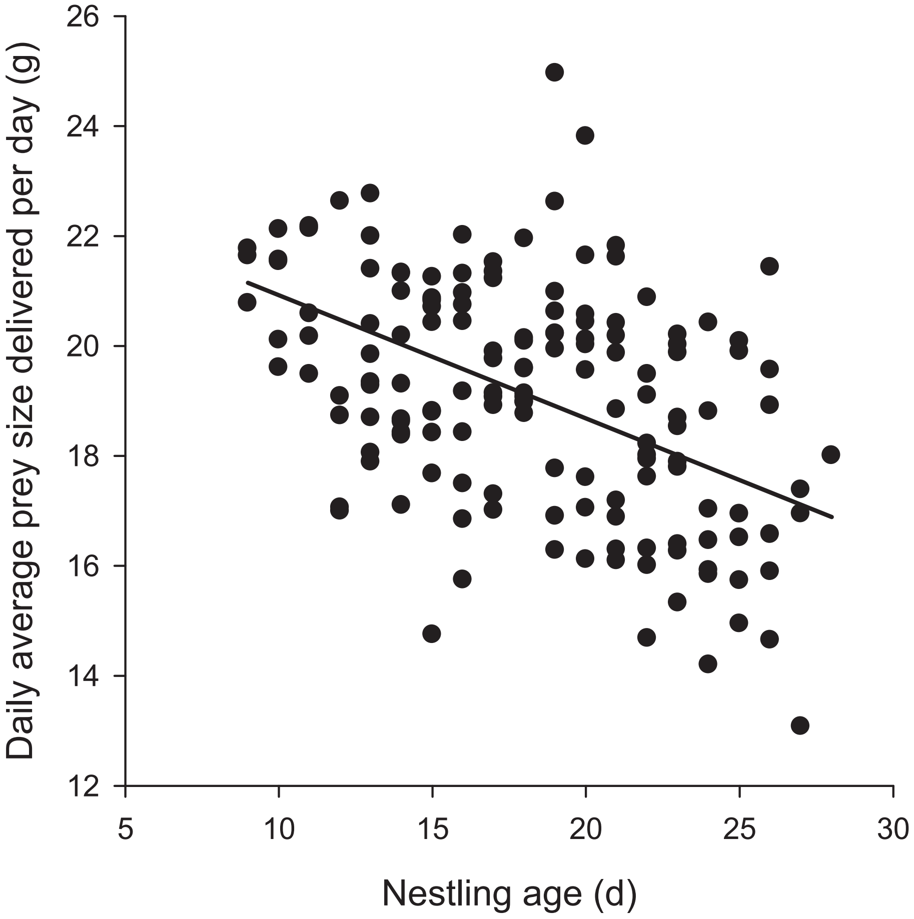

Figure 6. Daily average body mass of prey items delivered by parent Eurasian kestrels in relation to nestling age. The regression is calculated from the parameter estimates of the best fitted lme model (*f (x)* = 23.17 (CI=21.91-24.42) - 0.22 (CI=-0.28-(-0.17) *x*).

Paper VII

Should a raptor select small or large prey for its nestlings? Prey size and ingestion rate in breeding Eurasian kestrels *Falco tinnunculus*

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Abstract

Surprisingly little is known about how raptors handle their prey, although handling time affects prey profitability and hence also prey selection. By use of video we recorded handling time for 257 prey items provided to nestlings by nineteen pairs of the Eurasian kestrel (*Falco tinnunculus*). For a given type of prey (lizard, shrew, vole or bird) the variation in handling time was best explained by prey body mass. Ingestion rate was higher for large than small prey when the female fed nestlings, but not when the nestlings became able to feed unassisted. The most important reasons for this difference were probably that the female distributed the morsels from larger prey to several nestlings, so that any constraints set by the individual speed of swallowing would be relaxed, whereas when nestlings handled prey unassisted they often swallowed smaller prey whole. Smaller items were more likely to be monopolized when the nestlings fed unassisted. We suggest that as long as the female feeds the nestlings, kestrels should select larger prey items to maintain a high ingestion rate and an even distribution among brood mates. When the nestlings become able to handle prey unassisted it would be favorable to include smaller prey items in the diet, because these are then ingested at least with the same rate as larger ones. However, this benefit has to exceed potential costs of senior nestlings monopolizing small prey items.

Keywords: Eurasian kestrel, Falco tinnunculus, ingestion rate, nestlings, parent-offspring conflict, prey handling, prey selection, profitability, raptor.

Introduction

In altricial birds, the time spent food provisioning is constrained by many activities, such as territory guarding, nest defense, nest cleaning, brooding and resting (Grieco 2002, and references therein). Parents are assumed to maximize the total delivery to the brood, given the time constraints set by self-feeding and delivery (Ydenberg 2007). A constraint on delivery often neglected is the amount of time needed by parents to prepare the prey and feed it to the nestlings in suitable small pieces. Time spent preparing and ingesting a prey item usually constitutes a major part of the handling time, which determines prey profitability and hence influences prey selection (e.g., Sherry and McDade 1982; Stephens and Krebs 1986; Ydenberg and Hurd 1998).

When providing food for nestlings, altricial birds in general, and raptors (Accipitriformes, Falconiformes and Strigiformes) in particular, often prepare a prey item prior to delivery at the nest, and may even ingest part of it. Thus, the profitability of a prey cannot be estimated solely from observations of prey handling in the nest. Instead, a related ratio can be estimated, namely prey mass ingested per time unit spent on preparation and ingestion of the prey in the nest, either when a parent is partitioning the prey and feeding the nestlings with small pieces, or when the nestlings are feeding unassisted on prey delivered at the nest. This ratio, termed ingestion rate (cf. Slagsvold and Sonerud 2007), would suggest the ranking of different prey types in prey selection. However, this ranking would be prone to the error incurred by lack of data on time spent handling prior to delivery at the nest, i.e. capture, transport, and sometimes preparation and even ingestion of parts of the prey.

Ingestion rate has been found to decrease with prey size for self-feeding birds (Sullivan 1988; Grosch 2003), including raptors (Ille 1991; Slagsvold and Sonerud 2007). When raptors provide prey for their nestlings, there is usually a strict separation of sex roles the first weeks after hatching, with the female staying at the nest feeding the nestlings with the prey that the male has captured (Newton 1979). Later on, the nestlings become able to feed unassisted, and the female starts hunting. A senior nestling would then benefit from delivery of smaller prey, because it may more successfully monopolize such prey than larger ones (Anderson et al. 1993; Fargallo et al. 2003). To keep such monopolized prey, short handling time, and thus short exposure time of the item to competing nest mates, would be important.

Here we investigate if ingestion rate decreases with prey size also when raptors provide food to their nestlings in the wild. Obviously, information on ingestion rate of prey is important for predicting foraging strategies of raptors. We also investigate whether the ingestion rate as a function of prey size changes as the nestlings become able to feed unassisted, and discuss if a parent-offspring conflict may exist over prey size and distribution of food (cf. Trivers (1974); Kacelnik et al. (1995)). The Eurasian kestrel (*Falco tinnunculus*), hereafter called the kestrel, is a small raptor (male body mass c. 200 g) which feeds on a variety of prey, ranging from small to large prey (e.g. insects, lizards, shrews, voles and birds) (Village 1990). During the first two-three weeks after hatching, the male provides prey to the female, who then partitions the prey and feeds herself and the offspring (Village 1990). Later, also the female hunts, but she may still need to partition the prey to the young (Masman et al. 1988; Village 1990; Fargallo et al. 2003). In this study we used video to record handling of prey in kestrel nests to test whether the effect of prey mass on handling time (i.e. ingestion rate) differs between the four major prey types (lizard, shrew, vole and bird) when the female feeds dependent nestlings. If handling time increases relatively faster than prey mass for a prey type, it will be more efficient for the female to provide dependent nestlings with smaller prey items of that type. Further, we tested for factors affecting the probability that one nestling monopolizes a prey item when nestlings feed unassisted. Finally, we investigated whether the effect of prey mass on handling time (i.e. ingestion rate) differs between prey types being monopolized; if handling time increases relative faster per unit prey mass for a prey type, smaller prey items will be most efficient. We stress the importance of maximizing ingestion rate by individual nestlings because it means minimizing the time the item is exposed to competing nest mates per unit prey mass obtained.

Materials and methods

Study area and field methods

The study was conducted in the boreal and hemi-boreal zones in Trysil municipality, Hedmark county, southeast Norway (61º07´- 61º28´N; 12º06´- 12º43´E) during June and July in 2003 and 2005. Here >100 pairs of the kestrel breed in artificial nest boxes each year, of which we filmed nine in 2003 and ten in 2005. The boxes were located in clear-cuts and bogs, surrounded by coniferous forest with only minor patches of agricultural areas, mostly grazing land. Each nest was filmed for two days. In 2003, these days were two weeks apart; the nests were filmed first when brood age (mean age of the last hatched nestling) was 12.3±0.7 days (range 8-15, n = 9), and second when the brood age was 25.9±0.6 days (range 23-28, n = 8).

One day of recording failed in the second period. In 2005 the nests were filmed on two subsequent days, starting when brood age was 12.6±0.8 days (range 8-16, n = 10), with one exception; in one of the nests the second filming was conducted two days after the first. Mean brood size was 5.0±0.3 (range 4-7) in 2003 and 3.1±0.5 (range 1-5) in 2005.

In 2003, a mini-dv camcorder was used for the monitoring, whereas in 2005 an external CCTV camera was used in combination with the mini-dv camcorder. The total duration of video recorded was c. 390 hours. For each feeding session we identified the prey to type, i. e. whether it was an insect, a lizard (*Zootoca vivipara*), a shrew (Soricidae), a vole (Cricetidae), or a bird, for examples see supplementary material. Birds were further identified to species or genus. Of the 367 prey items recorded, 9 were classified as insect, 66 as lizard, 1 as frog (*Rana* sp.), 76 as shrew, 79 as vole, 129 as bird, 5 as unidentified small mammal and 2 as prey remain. The frog, the unidentified small mammals and the prey remains were excluded from the analyses due to low sample size (n = 8). Each feeding session was classified as either the female partitioning and feeding the nestlings (n= 212), or the nestlings feeding unassisted (n = 147). Among prey items handled by nestlings unassisted, we focused on prey being monopolized (n = 98) because handling time determines the exposure time of the item to competing nest mates. Of the remaining prey items, 45 were shared between two or more nestlings, 4 of the prey items could not be classified as monopolized or not.

Estimation of handling time

Handling time was defined as the time (measured to the nearest s) elapsing from when the female bent her head down to tear off the first piece until the item had been completely consumed or abandoned. If a nestling fed unassisted, it would either monopolize the prey item or share it with one or more siblings. For monopolized prey, feeding time was taken as the time elapsing from when the nestling lowered its head to tear off the first piece until the item was completely consumed or abandoned, or, if the prey item was swallowed whole, the time elapsing from when the nestling received the prey from the parent until its swallowing movements ended. If the female or nestlings stopped feeding for longer than 4-5 s, the pause was excluded from the feeding time.

Estimation of prey body mass

The body mass of lizards and small mammals has a relatively high intra-specific variation (Smajda and Majlath 1999; Norrdahl and Korpimäki 2002). Therefore, we estimated the body mass of each lizard and small mammal prey item delivered by the kestrels, rather than using an average mass for each species as has been done in previous studies (Fargallo et al. 2003; Laaksonen et al. 2004). We measured delivered prey items on a monitor as described by Steen (2004), Løw (2006) and Steen (2010). For common lizards, we used the regression model by Van Damme and Vanhooydonck (2001), $\log_{10}(\text{body mass}) = -1.767 + 3.201 * \log_{10}(\text{SVL})$, where SVL is snout-vent length. For small mammals we used a regression between body mass and size on the monitor obtained for specimen of the same species with known size and mass (Steen 2004; Løw 2006; Steen 2010).

The body mass of birds has a relatively small intra-specific variation; therefore a mean value for each prey species was obtained from data most pertinent to the breeding season in Fennoscandia (Cramp and Simmons 1980, 1983; Cramp 1985, 1988, 1992; Cramp and Perrins 1993, 1994a, b; Matthysen 1998; Selås 2001). If an avian prey was identified to genus only, as for instance many thrushes (*Turdus*) were, we calculated an average body mass of the possible species alternatives. For passerines, juveniles were given the same body mass as adults, whereas for grouse and shorebirds, the body mass of juveniles was estimated from form and relative size on the video frame. The estimated body mass of avian prey delivered at the nests is listed elsewhere (Steen 2004; Løw 2006). For the birds delivered decapitated, we subtracted 12.9 % of the body mass, based on the relative mass of heads removed by self-feeding raptors handling avian prey in captivity (T. Slagsvold and G. A. Sonerud, unpublished data). Most of the birds were plucked prior to delivery; i.e. a varying portion of the wings, tail and body feathers had been removed (Løw 2006). We did not correct the body mass for this removal, both because it was difficult to make a precise quantification of the mass of plucked feathers, and because this mass is rather minor according to studies of raptors in captivity (T. Slagsvold and G. A. Sonerud, unpublished data).

The mass-specific energy content of lizards, shrews, voles and birds are nearly similar, as is also the assimilation quotient, i.e. the assimilated portion of the energy content of the mass consumed (Masman et al. 1986; Karasov 1990; Tryjanowski and Hromada 2005). In terms of ingestion rate of a prey item we therefore used handling time as the currency (e.g., Rovero et al. 2000), and mass of the prey item delivered as the benefit of prey handling (e.g., Griffiths 1980).

In general, handling time is defined as the total time spent capturing, preparing and ingesting prey (e.g., Stephens and Krebs 1986; Kaspari 1990). Hence, if larger prey takes longer to prepare prior to delivery at the nest, for instance due to decapitating or plucking, our estimate of ingestion rate would overestimate the real ingestion rate of large prey. In fact, the probability that a prey item is decapitated prior to delivery at a kestrel´s nest increases with prey mass (Steen et al. 2010a). Voles and birds are often decapitated prior to delivery, but birds are also plucked (Village 1990). Thus, the cost of preparation is larger for avian prey than for voles. However, the parents sometime remove the intestines of voles prior to delivery at the nest (Masman et al. 1986). We did not quantify removal of intestines, but some voles delivered had their abdomen opened, indicating that the parent had removed entrails prior to delivery. These voles were excluded from the analysis (see above). However, the cost of removing parts of a vole may be compensated by the gain the parents get by eating the parts; they usually eat the head (Village 1990), and during breeding the female may eat the intestines (Masman et al. 1986). According to our own observations, the kestrel female also feeds the nestlings with the intestines from voles, and such intestines were never observed as remnants in the nest boxes, in contrast to feathers and legs from avian prey. However, to avoid disturbance, we did not visit the nests after each meal to collect and weigh prey remains.

For some prey items handling time was not obtained, either because the handling was difficult to view, because the prey item was not completely eaten, or because the handling was interrupted by prey delivery or tape change. Also, for some items the body mass could not be estimated, either because the prey was difficult to view, mainly due to quick prey delivery, or because the prey had been partly eaten prior to delivery (e.g. some voles were delivered with the abdomen opened). Of the 359 prey items classified as insects, lizards, shrews, voles or birds, 270 were assigned both an estimated body mass and a handling time. Of these items the female handled 167 (12 lizards, 27 shrews, 29 voles and 99 birds) and nestlings handled 103. Of the latter 103 items, 77 were monopolized by one nestling (9 insects, 37 lizards, 27 shrews, 4 voles) and 26 were shared between two or more nestlings participating in eating (none lizards, 4 shrews, and 11 voles).

Statistical analyses

Model selection and parameter estimation were performed with the software R, version 2.8.1 (R Development Core Team 2008), using linear mixed effect models (lme) with the function lme () based on restricted maximum likelihood of the parameters in the nlme package (Pinheiro and Bates 2000, R Development Core Team 2008).

For the cases, when the female was feeding nestlings, the response variable was handling time (s), and explanatory variables were prey mass (g), prey type (lizard, shrew, vole or bird), nestling age and brood size. For the cases, when a nestling was feeding unassisted on a prey it had monopolized, the response variable was handling time (s), and explanatory variables were prey mass (g), prey type (lizard swallowed whole, shrew swallowed, or shrew eaten in pieces), nestling age and brood size. Too few lizards were eaten in pieces (n = 7) to make a meaningful test, and voles and birds were excluded because no bird, and too few voles, with assigned body mass and handling time (n=4) were monopolized. Hence, the total number of observations for analyzing handling time of prey being monopolized was 57. Brood size and nestling age were considered as co-factors. Because the effect of prey mass on handling time represents ingestion rate (g/s), the main explanatory variables of interests in all tests were prey mass and the interaction between prey mass and prey type, i.e. whether the effect of prey mass on handling time differed between prey types (cf. Pinheiro and Bates (2000). In all models, co-factors were included in the final model only when being associated with a p-value smaller than 0.10. Nest ID was included as random effect in the models to control for non-independence of data from the same nest (Pinheiro and Bates 2000). Handling time and prey mass were $\log_{10}$ transformed to obtain approximate normal distributions. Although the random effect of nest ID was very low in all the lme models, the variable was always included to control for the effect of differences between nests.

In order to evaluate the effect of prey size on ingestion rate it is important to determine how handling time, and thus costs, increases with prey mass. If handling time increases faster than the increase in prey mass, i.e. if the slope of the log-log plot is significantly larger than one, the ingestion rate will be higher for smaller prey than larger prey (Sherry and McDade 1982). Hence, handling time ($\log_{10}$ transformed) was regressed on prey mass ($\log_{10}$ transformed), which gives the straight line $Y = \beta_0 + \beta x$. To control for contributions of other explanatory variables the values of $\beta_0 + \beta x$ and the associated 95% confidence intervals were calculated from the lme parameter estimates, using the function “intervals” in R (R Development Core Team 2008). We used the “treatment contrasts” function in R (R Development Core Team 2008) to test for changes from the first level of the factor to each of the other levels in the selected model (Pinheiro and Bates 2000).

To test how prey body mass affected the probability that a prey was monopolized by one nestling when the nestlings fed unassisted we used the generalized linear mixed effect model (glm) with the function lmer () by the Laplace approximation in the lme4 package (Pinheiro and Bates 2000). Of the 367 recorded prey items, the nestlings handled 147 prey items unassisted (9 insects, 50 lizards, 40 shrews, 30 voles, 18 birds), of which 98 of the prey items were monopolized (9 insects, 49 lizards, 34 shrews, 5 voles, and 1 bird), 45 were shared between two or more nestlings (6 shrews, 22 voles and 17 birds), and 4 (1 lizard and 3 voles) were not classified as monopolized or not. Of these prey items handled by the nestlings 118 were assigned an estimated body mass (9 insects, 41 lizards, 35 shrews, 20 voles and 13 birds), of these 84 were monopolized by one nestling (9 insects, 41 lizards, 30 shrews, 4 voles) and 34 were shared between two or more nestlings (5 shrews, 16 voles and 13 birds). Insects, lizards and birds were excluded from the analyses since all insects and lizards, and none of the birds, with assigned body mass were monopolized. Also, data from one nest with only one nestling were excluded (2 shrews). Hence, 33 shrews and 20 voles constituted the number of observations in the analysis. The response variable was whether a prey item was monopolized or not. Explanatory variables were prey type (shrew or vole), prey mass, nestling age, brood size, and the interactions between prey type and prey mass and between prey type and nestling age, with nest ID as random factor. Because we were seeking the most parsimonious explanation, explanatory variables were kept only if the AIC-value decreased with more than 2.0 after adding it to the model (Burnham and Anderson, 1998; Burnham, 2002).

Results

When the female fed the nestlings, handling time was explained by prey mass, and the effect differed almost significantly between prey types (Table 1a). Brood size and nestling age did not contribute to the model. The effect of prey mass for lizards was different from that for birds and voles (F_{141} = 6.65, P = 0.011, n = 167, and F_{141} = 3.52, P = 0.062, n = 167, respectively). A log-log plot of handling time and prey mass (Figure 1a) shows that handling time was significantly associated with prey mass for voles and birds only. The slope was significantly smaller than one for lizards (y = 2.05 - x*0.30 (95% CI = -0.95-0.35, n = 12) and birds (y= 1.52 + x*0.60 (95% CI = 0.39-0.81, n = 99), almost significantly smaller than one for voles (y = 1.56 + x*0.50 (95% CI = -0.02-1.01, n = 29), but not significantly smaller than one for shrews (y = 2.02 + x*0.05 (95% CI = -1.27-1.28, n = 27). Hence, if prey were lizards or birds the female feed the nestlings with a higher ingestion rate for larger items. This tended to be the case also when prey were voles, but not if prey were shrews. For an average prey mass, see below, ingestion rate (based on the parameter estimates in lme model) was 4.8 g/min for lizards, 5.3 g/min for shrews, 7.4 g/min for voles and 7.5 g/min for birds.

All insects (n = 9) and lizards (n = 40), 85 % of the shrews (n = 33), 20 % of the voles (n = 20) were monopolized, but none of the birds (n = 13). Estimated body mass of prey delivered at the nest was 0.2 g (n = 9) for insects, 5.4±0.3 g (n = 54) for lizards, 9.5±0.3 g (n = 64) for shrews, 19.3±1.2 g (n = 51) for voles, and 34.7±2.2 g (n = 118) for birds. Thus, the nestlings were more likely to monopolize the smaller prey types. The probability of monopolizing for mammals was best explained by prey type (vole or shrew), nestling age and prey mass (Table 2). For both prey types the probability for monopolizing decreased with nestling age and decreased with prey mass, in general, shrews were more likely to be monopolized than to voles (Fig. 2).

When the nestlings fed unassisted on monopolized prey, handling time was best explained by prey mass. The effect did not differ significantly among prey types (lizards, shrews swallowed whole or shrews eaten in pieces; Table 1b). Brood size and nestling age did not contribute to the model. A log-log plot of handling time and prey mass for lizards, shrews swallowed whole, and shrews eaten in pieces (Figure 1b) shows that handling time increased significantly with prey mass, but the slope did not differ significantly from one neither for lizards ($y = 0.77 + x*0.56$ (95% CI = -0.01-1.13, n = 29) nor for shrews swallowed whole ($y = 0.80 + x*1.33$ (95% CI = 0.02-2.64, n = 15) or in pieces ($y = 0.35 + x*1.79$ (95% CI = 0.36-3.21, n = 12). Hence, there was no difference in ingestion rate between ingesting smaller and larger prey of the same type when the nestlings swallowed prey whole. For an average prey mass ingestion rate (based on the parameter estimates in lme model) was 21.1 g/min for lizards being swallowed whole, 4.4 g/min for shrews being swallowed whole and 4.5 g/min for shrews being eaten in pieces.

Discussion

Ingestion rate when the female fed the nestlings and when nestlings fed unassisted

When the female fed the nestlings, handling time was explained by prey mass, and increased with mass for all prey types except lizards. Increasing handling time with increasing prey mass agrees with previous findings for birds (e.g. Salt and Willard 1971; Craig 1978; Griffiths

1980; Sherry and McDade 1982; Kaspari 1990). Ingestion rate was higher for larger prey items than smaller ones for all prey types except shrews. This is opposite to the pattern found for self-feeding raptors (Ille 1991; Slagsvold and Sonerud 2007). Further, it tended to be more efficient to feed the dependent nestlings with voles and birds than lizards and shrews.

Also when the nestlings fed unassisted on prey being monopolized by one nestling (lizards and shrews), handling time was best explained by prey mass. The effect of prey mass on handling time did not differ between lizards and shrews, and smaller and larger items were ingested with an approximately equal ingestion rate. On average, however, lizards were ingested with an higher rate than shrews, probably because they were smaller, and because furless cylindrical prey items may be easier to swallow than those with fur and larger appendages (cf. Craig 1978; Kaspari 1990; Barba et al. 1996). In line with this, we found that shrews were ingested with similar rate when being swallowed whole as when being eaten in pieces. We also found that the nestlings never swallowed voles or birds without prior partitioning.

Parent-offspring conflict

If prey selection is based on ingestion rate in the nest as estimated in our study, it would differ depending on whether the female kestrel feeds her nestlings or whether the nestlings handle prey unassisted. Thus, prey selection would depend on the stage of breeding. As long as the female feeds dependent nestlings, the parents should select larger items of a given prey type for delivery to the young, because a higher ingestion rate for larger prey items than smaller prey items, except in the case of shrews, and may also contribute to a more even distribution of food among the nestlings. However, even if avian prey were as efficient to handle in the nests as were voles, in general birds should be taken less than the other prey types due to longer handling time outside the nest. In particular, birds are plucked prior to delivery at the nest (Village 1990; Løw 2006), and the time needed for this preparation would add a considerably to the total handling time (G.A. Sonerud unpublished data). In contrast, when the nestlings become able to handle prey on their own, a senior nestling would benefit from delivery of smaller prey (lizards and shrews), because this would increase the probability of monopolizing the prey and achieving a higher ingestion rate. Further, by swallowing a prey item whole a nestling would also benefit from a shorter exposure time of the item to competing nest mates. Thus, a parent-offspring conflict may exist over prey size and distribution of food (cf. Trivers (1974); Kacelnik et al. (1995)).

Smaller prey items were more likely to be monopolized by one nestling. Hence, if the diet had consisted mainly of small prey, a dominant nestling would have obtained more food and developed faster than its siblings. However, this effect was most apparent the first week after the nestlings became able to feed unassisted, and was negligible when they were older than three weeks, when prey were voles or large shrews. This may be due to the fact that the nestlings become more active with age, and thereby compete more for a prey item, making monopolization more difficult.

We found the highest ingestion rate for lizards being swallowed whole. Fargallo et al. (2003) found that when female kestrels delivered whole prey items to c. 11 days old nestlings, the larger female offspring received more food than the smaller male offspring. Therefore, a size-based female dominance may affect nestling growth if parents provide small prey only. The female kestrel may prevent this by feeding more nestlings from one prey item and also by partitioning small prey items despite a longer handling time. Partitioning of prey may also lead to better assimilation of the food. Finally, a more regular intake of food by each nestling may be better for digestion than an irregular intake of a few large pieces.

The possible parent-offspring conflict suggested above may be influenced by inter-annual variation in access to prey, in particular voles, probably forcing parents to take whatever prey they encounter in years of low prey abundance. In kestrels, nestling competition is proposed to be stronger in years with low vole abundance, when the kestrels may feed more frequently on smaller prey items that can be monopolized by seniors, such as shrews and lizards (Fargallo et al. 2003).

Should parents select small or large prey?

We found that when the female fed nestlings, the ingestion rate of prey in the nest for the brood as a whole was higher for larger than for smaller items of lizards, voles and birds. This is opposite to what was found for self-feeding raptors in 217 trials with 18 individuals of seven species from three avian orders in temporal captivity (Slagsvold and Sonerud 2007). In a field study of self-feeding adult kestrels (Masman et al. 1986), 41 feeding sessions were observed for voles with known size. We extracted data from figure 1 in Masman et al. (1986), and calculated ingestion rate, which decreased with prey size, as for the raptors studied by Slagsvold and Sonerud (2007). When comparing these estimates with ours for the cases when the female fed nestlings (based on the parameter estimates in lme model), the values are very similar for smaller voles (4.7 vs. 5. 2 g/min for a 10 g vole), but not for larger (3.9 vs. 9.1

g/min for a 30 g vole). We suggest two explanations for why ingestion rate was higher for larger voles in our study than in that of Masman et al. (1986). First, the female fed the nestlings at a higher rate than would have been the case for self-feeding. This may be a consequence of the fact that she often delivered the morsels from a prey item to more than one nestling so that feeding may have been less constrained by time spent swallowing. Second, because of time constraints, the female may have delivered larger pieces of food to the nestlings than when feeding by herself. Partitioning of the prey items in smaller pieces may increase food assimilation, but also compete for time needed for other activities, such as brooding, self-feeding and hunting. Moreover, in our study older nestlings often chased the female when she arrived at the nest with a prey, and tried to grab the prey and feed from it on their own. The female may have tried to avoid this harassment by quick feeding of the nestlings.

Although we did not measure the amount of uneaten remains, our general impression was that these were few. Sometimes wings and legs from avian prey remained, but apparently no parts of small mammals were left. However, most likely the proportion of uneaten remains increased with prey size, and was larger for avian than mammalian prey, as found for self-feeding raptors in temporal captivity (Slagsvold et al. 2010). Adjusting ingested mass for uneaten remains would reduce the estimated profitability of larger prey, in particular avian prey.

When provisioning larger prey the female would pay a cost by being restricted to the nest to feed the nestlings for a longer period, compared to when provisioning small prey that the nestlings would be able to handle by themselves at an earlier age (G. A. Sonerud 2010). Hence, the family as a whole may benefit from parental provisioning of small prey also at relatively early nestling stages. For raptors that have a less extensive digestive tract than the kestrel and hence may need more careful feeding of the young, such as typical bird hunters like most falcons and *Accipiter* hawks (Barton and Houston 1993; Hilton et al. 1999), including small prey in the diet may be even more important.

In conclusion, during the first week after hatching when the kestrel female has to partition prey and feed dependent nestlings the male may select larger prey items, and in particular large voles, to ensure a high ingestion rate and an even distribution of food among the nestlings. On the other hand, when the nestlings become able to feed unassisted and swallow small prey whole in the second week after hatching, it would be favorable to include small prey in the diet, i.e. shrews and in particular lizards, because ingestion rate would be high, and because the female would be relieved from prey partitioning and allowed to hunt (cf. Slagsvold and Sonerud 2007). Indeed, in 2007, we found the kestrels to deliver smaller prey items when the nestlings grew older, but this may as well be cause by a seasonal effect (Steen et al. 2010b). Also, the kestrels seemed to capture lizards whenever they had the opportunity, as a prey item delivered were more likely to be a lizard with increasing ambient temperature and solar height (Steen et al. 2010c). However, the benefits of delivering small prey have to exceed the potential costs of senior nestlings monopolizing such prey.

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Table 1. Results from the lme models with handling time as response variable. A) Kestrel female feeding dependent nestlings with lizards, shrews, voles and birds (n = 167, 19 nests). B) Kestrel nestlings feeding unassisted (lizards swallowed whole, shrews swallowed whole, and shrews eaten in pieces, n = 44, 10 nests).

Explanatory variable		*df*	*F*	*P*
A.	Intercept	141	11536.46	<0.001
	Prey mass	141	24.70	<0.001
	Prey type	141	28.71	<0.001
	Prey mass*prey type	141	2.42	0.069
B.	Intercept	38	459.90	<0.001
	Prey mass	38	56.47	<0.001
	Prey type	38	15.41	<0.001
	Prey mass*prey type	38	1.60	0.213

Table 2. Logistic regression model of the probability that a prey item was monopolized by one kestrel nestling as a function of prey type (shrew and vole), prey mass and nestling age. Parameter estimates of the selected linear mixed effect model (with shrew as intercept for model b)), and with nest ID as random effects, (53 prey items, 11 nests).

Explanatory variables	*Estimate*	*SE*	*z-value*	*P*
(Intercept)	21.40	9.78	2.19	0.029
Prey	-2.30	1.26	-1.83	0.068
Mass	-0.22	0.14	-1.60	0.109
Age	-0.70	0.35	-2.00	0.045

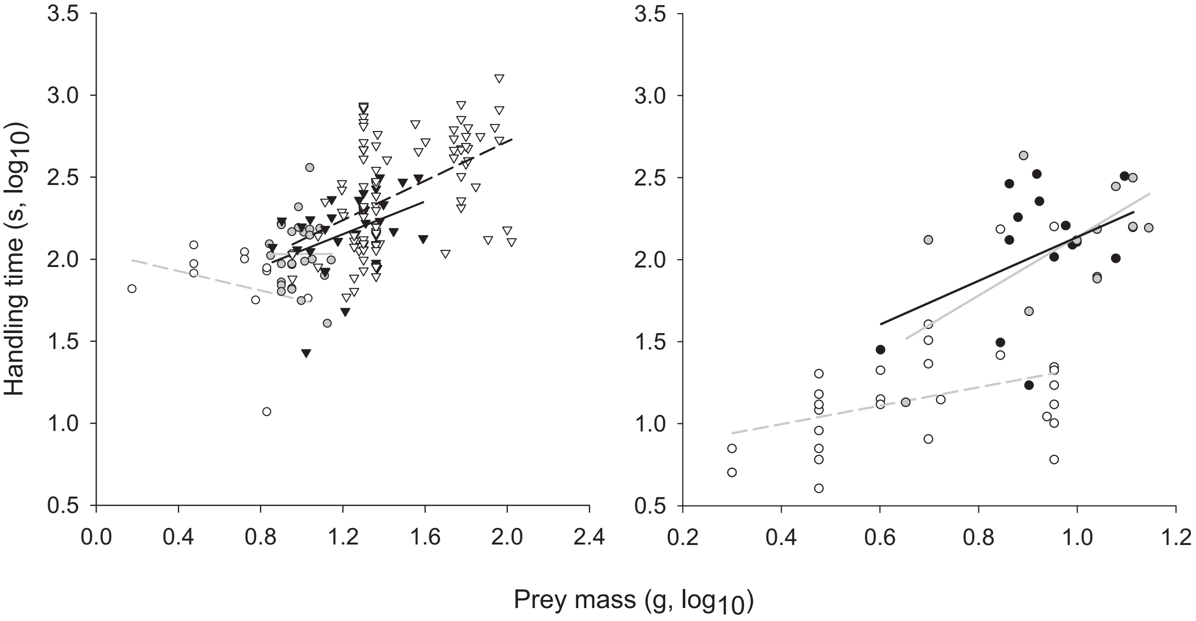

Figure 1. Regression of handling time on prey mass (log $_{10}$ transformed) for prey handled by kestrels in the nest. The regression lines are calculated from the parameter estimates in the lme model. a) The female feeding nestlings (all prey types); lizards (open circles, grey dashed line, $y = 2.05 - x*0.30$, $p = 0.372$, $n = 12$); shrews (grey circles, solid grey line, $y = 2.02 + x*0.05$, $p = 0.993$, $n = 27$); voles (black triangles, black line, $y = 1.56 + x*0.50$, $p = 0.060$, $n = 29$); and birds (open circles, dashed black line, $1.52 + x*0.60$, $p < 0.001$, $n = 99$). b) The nestlings handling prey unassisted; lizards being swallowed whole (open circles, grey dashed line, $y = 0.77 + x*0.56$, $p = 0.055$, $n = 29$); shrews being swallowed whole (black circles, black solid line, $y = 0.80 + x*1.33$, $p = 0.047$, $n = 15$) and shrews being eaten in pieces (grey circles, grey solid line, $y = 0.35 + x*1.79$, $p = 0.015$, $n = 12$).

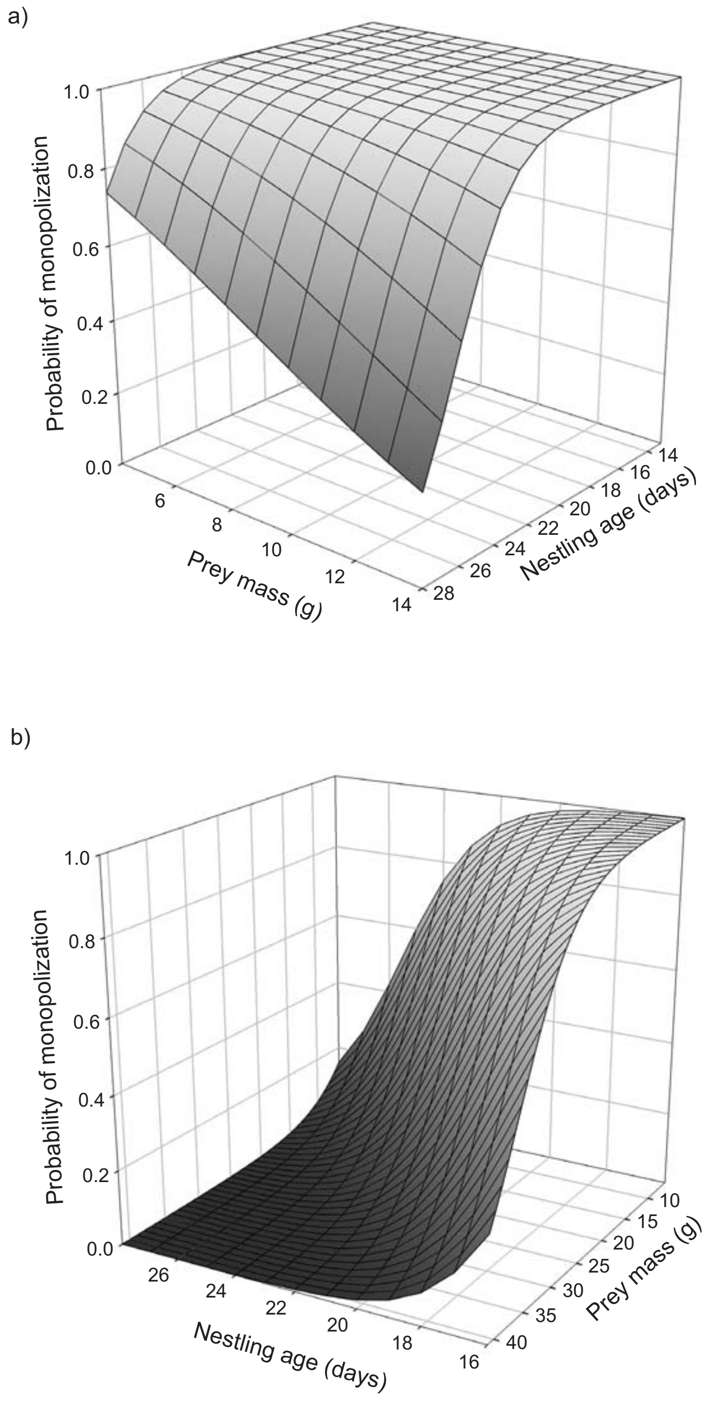

Figure. 2. The probability that a mammalian prey was monopolized by one kestrel nestling or shared by two or more nestlings as a function of prey body mass and nestling age, with the plane describing the complete logistic regression model, calculated from the parameter estimates in the glm model. a) Shrews. b) Voles. Note the different orientation of the x-axis and the y-axis between a) and b).

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