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.
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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

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 $\pm$ 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 $\leq$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.