



Evolution of parental roles in raptors: prey type determines role asymmetry in the Eurasian kestrel



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Raptors deviate from the norm among provisioning birds by having asymmetric parental roles, with the female brooding and feeding offspring, and the male providing food, assisted by the female from the latter part of the rearing period. To investigate the poorly understood evolution of role asymmetry in raptors at an intraspecific level, we videorecorded prey delivery and handling in 25 nests of the Eurasian kestrel, *Falco tinnunculus*, with prey types ranging in size from insects via lizards and mammals to birds, and simultaneously observed prey transfer from male to female outside the nest. As the nestlings aged, the male was more likely to allocate prey items directly to them for unassisted feeding, rather than to the female for further processing and feeding of the nestlings. This switch occurred earlier for lizards than mammals and birds, and earlier for smaller than larger mammals. The time needed to ingest a prey item decreased from birds via mammals to lizards, and was particularly short for insects. The switch from nestlings being fed dismembered prey to nestlings ingesting prey unassisted occurred earlier for lizards than mammals and birds, and earlier for smaller than larger mammals, while all insects were ingested unassisted. Thus, the female could be relieved from dismembering prey, and start hunting, earlier if all prey were lizards rather than mammals and birds, if all mammalian prey were smaller, and in particular if all prey were insects. Because providing for the family selects for small body size, extended confinement of the female as a sedentary food processor for offspring would leave greater potential for differential selection on male and female body size. This potential would vary geographically with the composition of the kestrel's diet, and be larger where the diet contains fewer insects and lizards and more mammals and birds.

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Among provisioning birds, raptors [hawks (Accipitriformes), falcons (Falconiformes) and owls (Strigiformes)] deviate from the norm through their asymmetric parental roles; in most species the female incubates, broods and feeds the nestlings, and the male hunts, assisted by the female from the latter part of the nestling period, if at all (Byholm, Rousi, & Sole, 2011; Cramp, 1985; Cramp & Simmons, 1980; Eldegard, Selås, Sonerud, Steel, & Rafoss, 2003; Eldegard & Sonerud, 2010, 2012; Newton, 1979, 1986; Wiehn & Korpimäki, 1997). The evolution of these asymmetric parental sex roles has been poorly understood (Andersson, 1994; Andersson & Norberg, 1981), but diet seems to have a key role (Slagsvold & Sonerud, 2007; Sonerud et al., 2014). Raptors represent an

excellent test system for how parental roles in birds providing for their offspring are affected by diet, because raptors capture not only insects and other relatively small invertebrate prey, as do most other provisioning birds including passerines, but also relatively large vertebrate prey (Newton, 1979), and thus prey with a wide range in body mass and ingestion time. Also, raptors are single-prey loaders, i.e. they carry one prey item at a time from the capture site to the nest (Sonerud, 1992), so that prey identity can be unambiguously assigned to prey load.

Provisioning for nestlings includes not only collecting food, but also preparing prey items so that they are a suitable size for ingestion. Most raptors take relatively large prey, which may be impossible for their nestlings to handle and hence require extended parental assistance in dismembering prey prior to feeding (Cramp, 1985; Cramp & Simmons, 1980; Newton, 1979, 1986). The morsels fed to nestlings are surprisingly small, e.g. 0.6 g for Eurasian kestrel, *Falco tinnunculus* (Fargallo et al., 2003). Therefore, raptors may need a long time to feed their nestlings from a prey item.

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The conflict between collecting and processing food for the nestlings may select for asymmetric parental roles. If both parents hunted and if both fed the young, longer feeding times would increase the probability that one parent would arrive with a prey item while the other was still feeding the young with another item. Waiting for the other parent to finish feeding the young would in general delay the resumption of foraging, and in particular delay any return to the site where the previous prey was captured, reducing the payoff of a win–stay hunting strategy (Sonerud, 1985). Leaving the prey item at the nest to be further handled by the mate who is already at the nest feeding the young, i.e. one sex specializing on hunting and the other on dismembering prey for the nestlings, may accelerate rates of prey capture and food transfer to nestlings. The constraint of long feeding times in raptors may thus strengthen any ancestral asymmetry in parental roles with the female as the main incubator and brooder (cf. Ketterson & Nolan, 1994). If this is true, the female's role as food processor should vary with feeding time, and hence with prey type and prey size if feeding time varies with prey type and prey size (Slagsvold & Sonerud, 2007).

At an interspecific level, Sonerud et al. (2014) demonstrated that female confinement to the nest was determined by diet: across nine raptor species the female dismembered prey and fed offspring for a longer portion of the rearing period as relative prey size increased. One of these raptor species, the Eurasian kestrel, is particularly well suited for a more detailed study, because its diet contains a wide range of prey types of varying size, including insects, reptiles, mammals and birds (Village, 1990). Here we therefore analysed the female's parental role in relation to prey type and prey size in more detail at an intraspecific level, using data on prey delivery and prey handling from kestrel nests.

METHODS

Study Area and Species

The fieldwork was done in June–July in 2003, 2005 and 2006 within a ca. 2000 km² area (61°07'–61°31'N, 12°00'–12°43'E) in the boreal zone in Trysil municipality, Hedmark county, southeast Norway. Here more than 100 pairs of the kestrel breed in nestboxes most years, of which nine were monitored in 2003, 10 in 2005 and six in 2006, in total 25. The average \pm SE distance to the nearest other monitored nest in the same year was 6.7 \pm 3.7 km (range 2.1–35.8) in 2003, 3.1 \pm 0.6 km (range 0.6–7.4) in 2005 and 6.9 \pm 4.7 km (range 0.6–29.8) in 2006. All nests were in boxes with an open front, deployed 5–15 m above ground in trees located in bogs, clear-cuts or open forest. The study area is covered by coniferous forest intensively managed by modern forestry. 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. The kestrel is also a migrant in western Finland (63°N), where 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 one nestbox was filmed both in 2003 and in 2005, and three boxes were filmed both in 2005 and in 2006, it is likely that different individuals were involved. When treating breeding pairs as a sample unit, therefore, we regarded the sample size as 25.

Recording Behaviour in the Nest

The nests were checked at least twice before video monitoring to determine hatching date. Each brood was filmed for 2 days,

except one in 2003, which was filmed for 1 day only. In 2003, the first filming was done when brood age (i.e. the age of the last-hatched nestling) was 12.3 \pm 0.7 days (range 8–15), and the second when brood age was 25.9 \pm 0.6 days (range 23–28). In 2005, each brood was filmed on 2 consecutive days with one exception, first when brood age was 12.6 \pm 0.8 days (range 8–16), and second when brood age was 13.8 \pm 0.8 days (range 9–17). In 2006, each brood was filmed on 2 days, starting when brood age was 13.3 \pm 0.6 days (range 12–15). Brood size was 5.0 \pm 0.3 (range 4–7) in 2003, 3.1 \pm 0.5 (range 1–5) in 2005 and 4.5 \pm 0.3 (range 3–5) in 2006.

In 2003, a digital camcorder was mounted on top of the nestbox, with the lens pointing through the roof and towards the open front. A dummy camcorder was mounted in the same position 1 day prior to filming to habituate the kestrels. In 2005 and 2006, each original nestbox was replaced with a plywood nestbox specially made for filming with a camera top containing a CCTV lens, connected with a 50 m cable to a digital camcorder in a hide on the ground. This was done 2–4 days prior to filming to habituate the kestrels. For the nests filmed in 2003 and 2005, Steen, Løw, Sonerud, Selås, and Slagsvold (2010) describe the camera set-up and the video equipment in detail. For the nests filmed in 2006, the set-up was as in 2005, except for the camcorder being substituted by a time-lapse videocassette recorder (three nests) or by a hard disk drive recorder (three nests) as recording equipment. In all cases, the lens view allowed us to see the prey from when it was delivered by one of the parents until it was ingested by the nestlings. Different set-ups between years were a consequence of technical improvement, and all set-ups allowed us to recognize prey items delivered at the nests.

Recording Behaviour Outside the Nest

On each filming day at the kestrel nests in 2003 and 2005, i.e. at 19 of 25 kestrel nests filmed, the parents' allocation of prey prior to delivery at the nest was observed from a blind on the ground simultaneous with the video recording. The observations from the blind and the video recordings each covered 192 h in 2003 and 200 h in 2005. Sonerud et al. (2013) describe the surroundings of these kestrel nests in more detail.

For each prey item delivered at the nest, we scored time, type of prey (if possible; see below), the sex that captured the item and the sex that delivered the item. By synchronizing the observers' watches with the time recorder in the camcorder, we could later verify observed as well as suspected deliveries when watching the videos. Sex identification was unambiguous because the kestrel is sexually dichromatic (Village, 1990). The male was defined to have captured a prey if one of the following conditions was fulfilled. (1) The male was observed delivering the prey at the nest (females never deliver prey to males). (2) The male had been observed delivering the prey to the female outside the nest. (3) The female had been recorded arriving with a prey item at the nest without the male being observed, but his calling had been heard. The female was defined to have captured the prey if she had been recorded arriving with a prey item at the nest without the male being observed or his calling heard prior to delivery. Prey deliveries from male to female mostly occurred near the nest, and the male usually vocalized in a special way prior to delivery (cf. Village, 1990). The open landscape around the nestboxes made prey deliveries fairly easy to record from the blind, unless there was strong wind that made the male's calling difficult to hear.

Video Analysis

The video recordings were analysed on a monitor. For each delivery and subsequent feeding session recorded on the video, the

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