

Age at first breeding and fitness in goshawk *Accipiter gentilis*

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Summary

1. Age at first breeding has a large influence on fitness and hence is crucial to the evolution of life-history strategies. Goshawks *Accipiter gentilis* start breeding aged 1–4 years. Using 30 years of data and both lifetime reproductive success (LRS) and λ_{ind} as a fitness estimate for 74 female goshawks, I showed that the optimal age at first reproduction was 3 years in this population.

2. Females that started to breed earlier had lower LRS and λ_{ind} , not because of reduced life span, but because of lower reproduction at early ages.

3. The constraint hypothesis, which states that foraging or other skills improve with age was the most likely explanation for the higher reproduction with increasing age.

4. Incorporating habitat heterogeneity provided the mechanism that explained not only the fitness cost to early maturity, but also why this cost was heterogeneous. Females starting to breed aged 1 suffered a very high fitness cost if they were in a bad-quality territory, but fitness costs were small when they were in a good-quality territory. This explains why I found evidence for a nonlinear selection pressure on age at first breeding.

5. Population density also affected whether a female started to breed early or not: over the study period, population density increased and the percentage of females starting to breed aged 1 decreased.

6. The optimal age at first breeding seems to be a trait affected by a complex interplay between cost and benefits of early reproduction mediated by habitat heterogeneity and population density.

Key-words: delayed maturity, fitness, life-history evolution, selection, territory quality.

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Introduction

The age at which an organism starts to reproduce is considered an important life-history trait with a profound influence on fitness (Cole 1954; Lewontin 1965; Roff 1992; Stearns 1992; Charnov 1997; Brommer, Pietiäinen & Kolunen 1998; Prevot-Julliard *et al.* 1999). The benefits of an early start to reproduction include an increased probability of realizing reproduction and hence an increased fitness compared with a later start (McGraw & Caswell 1996; Oli, Hepp & Kenamer 2002). However, delayed maturity might be favoured if the costs of early reproduction, in terms of reduced survival, future reproduction or somatic growth, outweigh the benefits (Cody 1971; Stearns 1989; Weimerskirch

1992; Pyle *et al.* 1997; Tavecchia *et al.* 2001). The fitness consequences of this delayed maturity have received considerable theoretical (Caswell & Hastings 1980; Stearns & Koella 1986; Charnov 1997) and empirical (Lunn, Boyd & Croxall 1994; McGraw & Caswell 1996; Brommer *et al.* 1998; Oli *et al.* 2002) attention. This trade-off should lead to the evolution of an optimal age at first reproduction (Roff 1992; Stearns 1992).

In many long-lived, iteroparous organisms, individuals commonly do not start breeding as early as they are physiologically able to (Fisher 1975; Weimerskirch 1992; Pyle *et al.* 1997; Nielsen & Drachmann 2003). This has been interpreted as evidence that the costs of early breeding might be higher than the benefits (Weimerskirch 1992; Pyle *et al.* 1997). The results have been equivocal: the conclusions, by and large, being affected by which fitness estimate has been used (Oli *et al.* 2002). Studies using lifetime reproductive success (LRS) have generally not detected a cost of delayed maturity (Fitzpatrick & Woolfenden 1988; Newton 1988;

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Sternberg 1989; Viallefont, Cooke & Lebreton 1995; Pyle *et al.* 1997), while those using a recently developed rate-sensitive fitness measure (λ) predominantly found that early maturity should be favoured by selection (Ribble 1992; McGraw & Caswell 1996; Oli *et al.* 2002).

It is equally important to understand the proximate mechanisms creating differences in vital rates in relation to age (Martin 1995). Reproductive performance and survival commonly increase with age (Sæther 1990; Lunn *et al.* 1994; Forslund & Pärt 1995; Reid *et al.* 2003) and the strength of this increase will greatly influence whether early or delayed maturity will be favoured by selection. Four hypotheses, which are not mutually exclusive, try to explain improved reproductive performance with age (Forslund & Pärt 1995; Laaksonen, Korpimäki & Hakkarainen 2002).

The differential mortality hypothesis (Nol & Smith 1987) suggests that poor-quality individuals die earlier than high-quality individuals, hence any given cohort includes proportionally more high-quality individuals at later ages. The delayed breeding hypothesis (Hamann & Cooke 1987) proposes that high-quality individuals delay first breeding and recruit into the population at a later age. The constraint hypothesis (Curio 1983) suggests that individuals improve in reproductive performance through accumulation of breeding experience (Wooller *et al.* 1990) or more efficient foraging (MacLean 1986; Catry & Furness 1999). The restraint hypothesis (Williams 1966) predicts that reproductive effort increases with age because residual reproductive value decreases.

More illustrative than answering whether early or late maturity is optimal is to understand what mechanism has influenced one or the other strategy to be optimal (Martin 1995).

The goshawk *Accipiter gentilis* (Linnaeus) is a long-lived, medium-sized avian predator breeding all over the Holarctic (Cramp & Simmons 1980). It opportunistically feeds on birds and mammals, and individuals commonly start their breeding career when they are between 1 and 4 years old (Glutz von Blotzheim, Bauer & Bezzel 1971; Cramp & Simmons 1980; Fischer 1983). Using data from a 30-year study and estimating fitness using both LRS and individual λ , I asked whether (i) there is an optimal age at first reproduction, and (ii) what mechanisms might affect the costs and benefits associated with early or delayed maturity.

Materials and methods

DATA COLLECTION

Data for this study were collected from 1975 to 2004 in a 250-km² investigation area in Germany (52°10'N and 8°25'E; see Krüger & Lindström 2001a for details). Each year, all forest patches were visited and checked for goshawk activity. Between six and 18 goshawk breeding pairs were found annually, with the lowest densities in the early 1980s and higher densities in the 1990s (Krüger & Lindström 2001a). Each active nest was

visited at least three (normally five to 10) times a year to determine breeding success (success or failure) and brood size (number of chicks fledged) for successful breeding attempts. Data were collected through careful and intensive observation from the ground, hence nests were not climbed. Nevertheless, this method allowed reliable data collection (Krüger & Lindström 2001a; Nielsen & Drachmann 2003).

In goshawks and sparrowhawks, the pattern on the primary feathers is a reliable way of identifying individual birds and has been used repeatedly (Opdam & Müskens 1976; Newton & Marquiss 1982; Kühnapfel & Brune 1995; Bezzel, Rust & Kechele 1997; Nielsen & Drachmann 2003). Breeding females start moulting while incubating, so moulted primaries and secondaries can be found below or near the nest tree. Sufficient moult feathers were available over successive years to determine securely the life span of 74 females that started and finished their breeding career between 1980 and 2003. Age at first breeding was also determined from moult feathers, as they allow for a distinction between ages 1, 2, 3, and 4 based on both colour pattern and how faded the bars of the feather are. Several other studies have used this technique in *Accipiter* species to age individuals and study age-specific patterns in vital rates (Opdam & Müskens 1976; Kühnapfel & Brune 1995; Rust & Kechele 1996; Bezzel *et al.* 1997; Nielsen & Drachmann 2003). Individual identification and ageing of feathers was not done by the author but by someone with 30 years of experience in ageing feathers and determining female identities (Ulrich Stefener) who was blind to the hypotheses being tested.

Goshawks show a very high territory fidelity (Cramp & Simmons 1980; Fischer 1983); a movement between two neighbouring territories was observed only twice over the 30 years. Nevertheless, feathers found in a given territory in year t were always compared with all feathers found in the entire study area in year $t + 1$. Because goshawks occasionally skip a breeding attempt, individuals were only classified as dead if they were not found breeding in the study area for at least 2 years (Newton 1989; Nielsen & Drachmann 2003). Moult feathers were not found with the same regularity for males, hence no attempt was made to determine their life span and fitness.

DATA ANALYSIS

Reproductive variation in relation to age was assessed in two ways. First, age-specific reproduction data were compared using a generalized linear mixed model (GLMM) where female identity and year were included as random factors. Because the reproductive output as the dependent variable included failed breeding attempts, a Poisson error structure and log link function were used (Nielsen & Drachmann 2003). As a change in reproduction with age could be due to poor-quality individuals successively disappearing from the population (Nol & Smith 1987), the analysis was also repeated using only the few long-lived individuals (> 5 years).

The data did not allow the survival rate from birth to age 1 to be estimated. Instead, an estimate specific to western Germany was obtained from the literature (Cramp & Simmons 1980). To obtain survival rate estimates for other ages, mark–recapture models were used, where the first appearance of a moult feather from a given female was taken as the capture event and findings of moult feathers in later years equate to a recapture, as implemented in the program MARK (White & Burnham 1999). Individuals were recorded as present (moult feather found) or absent (no reliable identification through moult feather possible) within the breeding season. A Cormack–Jolly–Seber model was fitted (Lebreton *et al.* 1992) to obtain age-specific survival estimates. Model performance was assessed using the Akaike Information Criterion, corrected for small sample sizes (AICc, Burnham & Anderson 1998). As the fully time-dependent model had a significantly higher AICc (524.1 for the time-dependent model with 33 parameters vs. 498.3 for the time-independent model with 10 parameters), the survival estimates were hence generated using a time-independent model. This model ($\phi(\text{age})P(\cdot)$) fitted the data well, as assessed by a bootstrap goodness-of-fit test ($P = 0.27$). The variance inflation factor \hat{c} , quantifying data overdispersion, was calculated as the observed model deviance divided by the mean bootstrapped deviance. The value of \hat{c} was 1.061, indicating minimal overdispersion (Cooch & White 1998). Given the very high territory fidelity in goshawks (Cramp & Simmons 1980; Nielsen & Drachmann 2003), variation in survival probability most likely reflects variation in mortality rather than any dispersal effects.

Two different fitness measures were used in the analyses. LRS sums the offspring production over an organism's lifetime and is commonly used (Clutton-Brock 1988; Newton 1989; Brommer *et al.* 1998; Krüger & Lindström 2001b). A more recently derived fitness estimate is λ_{ind} , which is the dominant eigenvalue of a projection matrix consisting of age-specific fertility (multiplied by 0.5 to estimate the genetic contribution) and survival (McGraw & Caswell 1996). λ_{ind} is the growth rate of the phenotype of an organism in the population. One major difference between λ_{ind} and LRS is that λ_{ind} is rate-sensitive; it takes account of the timing of reproductive events as well as their outcome (McGraw & Caswell 1996). However, it is not always clear that λ_{ind} outperforms LRS as an estimate of fitness (Brommer, Merilä & Kokko 2002), and so both were used here.

Whenever LRS was statistically analysed, the log-transformed data were used. Establishment of the selection surface for λ_{ind} followed the approach of Lande & Arnold (1983), as implemented by McGraw & Caswell (1996).

Territory quality was estimated as the number of times a territory was used between 1975 and 2004 (see also Korpimäki 1992; Laaksonen *et al.* 2002). The underlying assumption is that often used territories are better than rarely used ones, a condition predicted by the ideal pre-emptive distribution (Pulliam & Danielson 1991). Elsewhere (Krüger & Lindström 2001a; Krüger

2002), it has been shown that this assumption holds for this goshawk population. This measure of territory quality is also not significantly affected by individual quality, given that the study lasted 30 years, while females had a mean number of breeding years of only 2.8, with a maximum of 9. Hence, a territory defined as good was not simply good because a long-lived individual had occupied it, because a threshold value of 12 years of occupation was used to separate a good territory from a bad one. To reduce further the problem of circularity, I used mean LRS of all females breeding in a given territory in this analysis and excluded all territories that were only occupied by a single individual female. In addition, good-quality territories as defined by occupancy frequency have been shown to have higher brood sizes (Krüger & Lindström 2001a) and habitat features different from bad-quality territories, such as a higher habitat diversity and a greater distance of nests to human disturbances such as roads and houses (Krüger 2002).

Results

AGE-SPECIFIC PATTERNS OF VITAL RATES

Goshawk females showed significant differences in their reproductive output in relation to age (Fig. 1a). Reproduction rate increased almost threefold from 0.7 juveniles per breeding attempt at age 1, to 2.0 juveniles per breeding attempt at age 8. The GLMM found no significant effects of year ($\chi^2 = 0.941$, d.f. = 1, $P = 0.544$) or female identity on reproductive output ($\chi^2 = 0.998$, d.f. = 1, $P = 0.484$), but there was a significant effect of

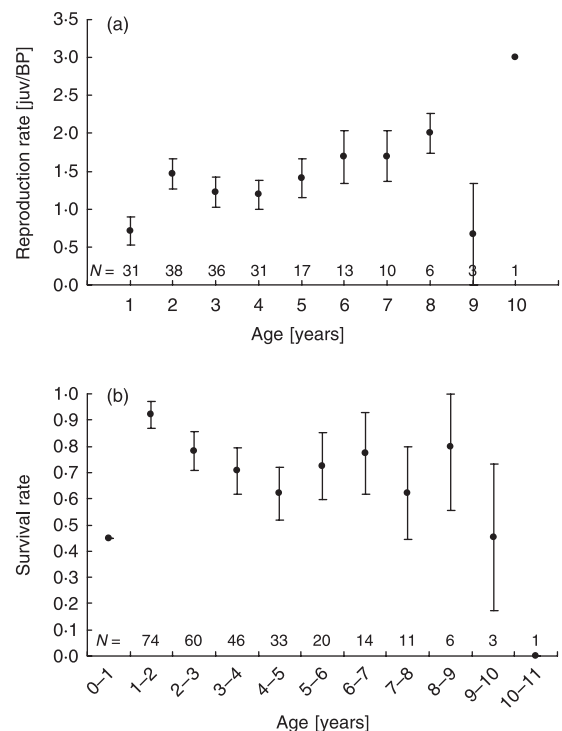


Fig. 1. Changes in (a) reproduction rate (juveniles per breeding attempt) and (b) estimated survival rate in relation to age. Values in (a) and (b) are means \pm SE.

age ($\chi^2 = 7.110$, d.f. = 1, $P = 0.008$). There was no evidence for a nonlinear effect of age on reproductive output ($\chi^2 = 0.431$, d.f. = 1, $P = 0.980$).

This increase in reproductive output was not due to poor-performing individuals disappearing from the population, because restricting the analysis to the few long-lived females (age > 5 years) showed that there was still no significant effect of female identity in the GLMM ($\chi^2 = 1.250$, d.f. = 1, $P = 0.239$) and they had a lower reproductive output from ages 1–4 ($\bar{x} = 1.35 \pm 0.20$ juveniles per breeding attempt) compared with ages 5–10 ($\bar{x} = 1.73 \pm 0.16$ juveniles per breeding attempt), although this difference was not significant any more in the GLMM ($\chi^2 = 2.140$, d.f. = 1, $P = 0.144$).

Reproductive output did not increase with breeding experience. Females starting their breeding career at age 2 had a similar reproductive output compared with individuals breeding for the second time at age 2 ($F_{1,37} = 0.009$, $P = 0.927$). Females starting their breeding career at age 3 also had a similar reproductive output compared with individuals breeding for the second or third time at age 3 ($F_{2,34} = 1.041$, $P = 0.364$). Moreover, females starting at age 4 had a higher reproductive output than those breeding for the second, third, or fourth time ($F_{3,27} = 5.760$, $P = 0.004$). However, there was also a significant difference in reproductive output with regard to age in first-time breeders ($F_{3,69} = 3.588$, $P = 0.018$), indicating that females delaying their first breeding attempt obtained a higher reproductive output in the first breeding attempt by doing so. Results also did not change if breeding experience was analysed together with female identity and age in a GLMM: experience as a variable was not significant ($\chi^2 = 1.440$, d.f. = 1, $P = 0.230$).

Survival rate estimates fluctuated between 62 and 92% between ages 1 and 8, dropped sharply at age 9 and no female survived beyond age 10 (Fig. 1b). For those ages where breeding can occur (1–10), survival decreased significantly with age ($r_8 = -0.718$, $P = 0.019$). There was also a trend for survival rate estimates to be correlated negatively with reproductive output across age ($r_8 = -0.608$, $P = 0.062$).

FITNESS ESTIMATES IN RELATION TO AGE AT FIRST BREEDING

Of the 74 goshawk females, 31 (41.9%) started their breeding career in the first year, 26 (35.1%) in the second, 10 (13.5%) in the third, and seven (9.5%) in the fourth year of life. The distribution of years as a breeder was highly skewed ($P < 0.001$) and ranged from 1 to 9 with a median of 2 years. LRS varied between 0 and 14 chicks, with a median of two chicks and λ_{ind} varied between 0 and 2.186 with a median of 1.0. Age at first breeding had a significant effect on LRS (Fig. 2a, $F_{3,70} = 3.043$, $P = 0.034$): those females starting their breeding career at age 3 produced, on average, twice as many offspring over their lifetime as females starting at age 1. The correlation between LRS and age at first

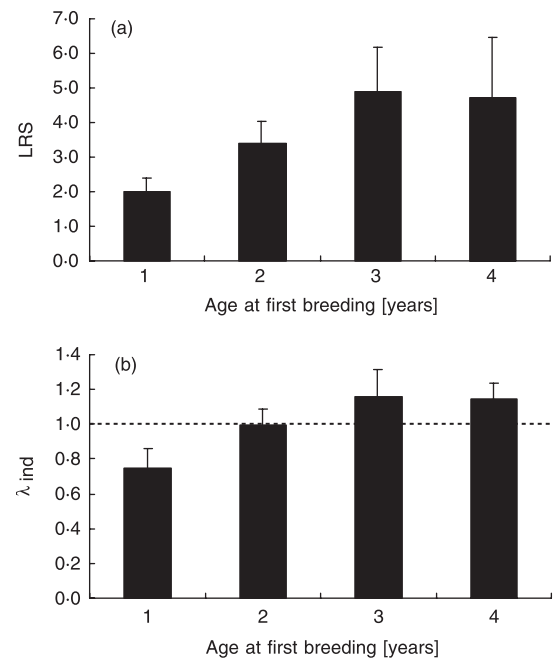


Fig. 2. Differences between females starting to breed at different ages in terms of (a) lifetime reproductive success (LRS) and mean individual fitness λ (b). Values are mean \pm SE. The dashed line in (b) at $\lambda = 1$ separates sink ($\lambda < 1$) from source ($\lambda > 1$) fitness values.

breeding was also significant and positive ($r_{72} = 0.322$, $P = 0.005$). This difference in LRS between different ages at first breeding was not caused by significant differences in breeding life span (Kruskal–Wallis test: $\chi^2 = 0.607$, d.f. = 3, $P = 0.895$). Using λ_{ind} as the fitness estimate changed the results little (Fig. 2b). Mean λ_{ind} for females starting their breeding career at age 1 and 2 was below 1, indicating sink phenotypes, while mean λ_{ind} of females starting at age 3 and 4 was above 1, indicating source phenotypes. While there was only a statistical trend between λ_{ind} and age at first breeding when analysed using ANOVA ($F_{3,70} = 2.302$, $P = 0.085$), there was a significant positive correlation between the two variables ($r_{72} = 0.272$, $P = 0.019$). This indicates that selection should favour a higher age at first breeding.

As both LRS and age at first breeding can be considered phenotypic traits influencing λ_{ind} (McGraw & Caswell 1996), the selection surface shows how they shape λ_{ind} in this goshawk population (Fig. 3a). Because this analysis focuses on the influence of realized phenotypic traits on fitness, LRS values were used and not the survival-corrected LRS values. There was directional selection favouring large LRS ($\beta = 1.793$, SE = 0.092, $t = 19.302$, $P < 0.001$) and higher age at first breeding ($\beta = 0.248$, SE = 0.114, $t = 2.172$, $P = 0.033$). In addition, there was evidence for stabilizing selection on LRS (quadratic term $\gamma = -0.727$, SE = 0.099, $t = 7.293$, $P < 0.001$) and disruptive or nonlinear selection on age at first breeding (quadratic term $\gamma = 0.154$, SE = 0.070, $t = 2.193$, $P = 0.032$). Furthermore, there was a negative interaction between LRS and age at first breeding ($\gamma = -0.302$, SE = 0.114, $t = 2.636$, $P = 0.010$), indicating

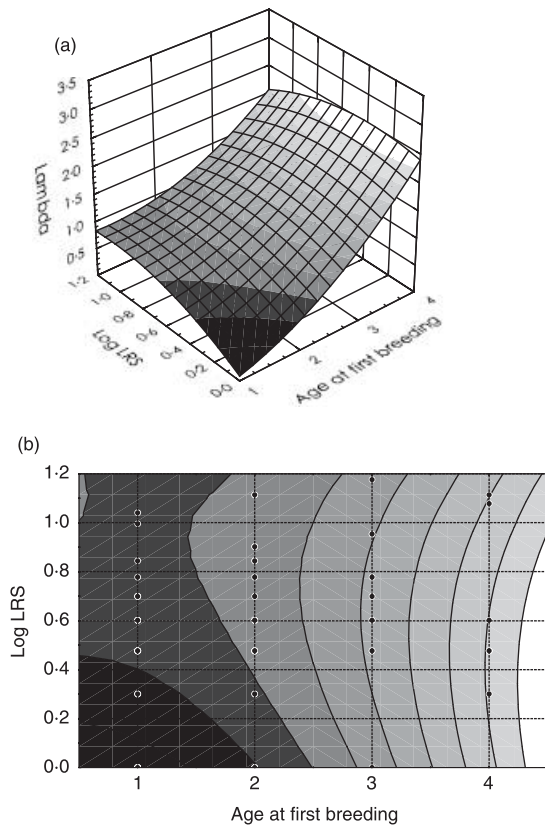


Fig. 3. Selection surface of individual fitness λ as a multiple regression function of lifetime reproductive success (LRS) and age at first breeding as phenotypic traits, using both linear and quadratic terms (a). Bird's eye view of the selection surface (b), showing the area of the character space occupied by individuals (dots) in the goshawk population. Fitness increases from black over levels of grey to white.

selection for an early age at first breeding coupled with high LRS values. The selection contours (Fig. 3b) indicate that most of the character space defined by LRS and age at first breeding is occupied by individuals. Across the character space occupied by individuals, it seems that the significance of the quadratic age term is not indicative of disruptive selection but rather of non-linear selection favouring a higher age at first breeding. Given these strong selection pressures to delay first breeding, it remains enigmatic why a sizeable proportion of females start to breed aged 1.

To address this puzzle, the influence of territory quality has to be incorporated into the analysis. Territory quality was positively correlated with the mean LRS of all females breeding in a given territory (Fig. 4a, $r_{18} = 0.465$, $P = 0.041$). This means either that territory quality influences LRS independently of individual quality or that good-quality territories are occupied constantly by higher-quality individuals compared with bad-quality territories. Combining territory quality and age at first breeding (Fig. 4b) indicated that females breeding in a bad-quality territory at age 1 failed to obtain any LRS much more often than those starting at age 1 in a good-quality territory ($\chi^2 = 4.385$, $P = 0.022$). No such significant difference between territory qualities was apparent

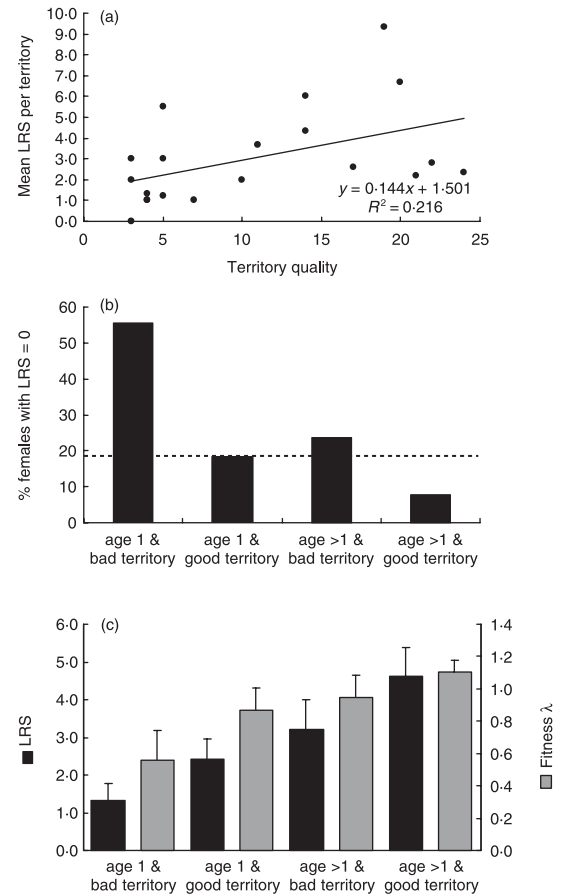


Fig. 4. Mean lifetime reproductive success (LRS) of all females breeding in a given territory in relation to the quality of that territory (a). Percentage of females failing to obtain any fitness (LRS = 0) in relation to age at first breeding and territory quality (b). Mean LRS and fitness λ in relation to age and territory quality (c). Error bars are SE.

for females starting their breeding career above age 1 ($\chi^2 = 2.067$, $P = 0.099$). Largely due to the higher percentage of females obtaining zero fitness in bad quality territories, there were significant differences in both LRS ($F_{3,70} = 4.196$, $P = 0.009$) and λ_{ind} ($F_{3,70} = 2.770$, $P = 0.048$) between the four categories (Fig. 4c). This explains the strong selection pressure for an apparent optimal age 3 at first breeding (Fig. 2c) and also the discrepancy between the observed distribution of ages at first breeding and the fitness differences. Females starting their breeding career at age 1 only paid a high fitness cost if they were in a bad-quality territory.

One additional factor explaining the mismatch between the observed frequency distribution of age at first breeding and the fitness difference is population density. Population density in the first year of breeding was negatively correlated with LRS ($r_{72} = -0.235$, $P = 0.044$) and also more females aged 1 entered the breeding population during the low-density years of the 1980s compared with the higher density years of the 1990s (dividing the period 1980–99 into five 4-year periods, the percentage of females aged 1 entering the breeding population decreased significantly over time: $r_3 = -0.919$, $P = 0.027$).

Highest fitness was still obtained when females started their breeding career at a higher age and in a good-quality territory. In fact, from the λ_{ind} values it seems that the observed population growth in this population comes largely from females starting their breeding career later than age 1 and in a good-quality territory, because this category is the only one with a mean λ_{ind} above 1, indicating source phenotypes.

Discussion

Female goshawks that entered the breeding population aged 2, 3, or even 4 years old had a higher fitness than those females starting to breed at age 1. This effect was not related to the fitness estimate used, LRS or λ_{ind} , which has traditionally been invoked to explain conflicting results (McGraw & Caswell 1996; Brommer *et al.* 2002; Oli *et al.* 2002). The reason why delayed maturity is favoured in this goshawk population is not due to differences in life span (see Oli *et al.* 2002 for an example of this effect), but due to differences in reproduction. The profound changes in reproductive performance with age are responsible for higher fitness in individuals with delayed maturity.

Which of the four hypotheses can explain changes in reproductive performance with age in this population? The differential-mortality hypothesis is not supported by our data as the interindividual pattern is similar to the intraindividual pattern, hence there is no systematic disappearance of poor-quality individuals from the population at young age. There is some evidence for the delayed-breeding hypothesis, because females starting their breeding career aged 4 had higher reproductive success than those of the same age, but with previous breeding experience. This effect was not significant for females aged 3 though. With regard to the constraint hypothesis, previous breeding experience did not increase reproductive performance (it actually decreased for females aged 4). However, there was an effect of age *per se*, as there were significant differences in the first breeding attempts of females aged 1–4. This might indicate that age improves performance through more efficient foraging skills (MacLean 1986), a factor of paramount importance for the aerial-hunting goshawk (Glutz *et al.* 1971; Newton 1979; Fischer 1983; Nielsen & Drachmann 2003). There was weak support for the restraint hypothesis. Survival decreased systematically with age in adults (excluding survival from birth to age 1), there was a systematic increase in reproduction with age and the two traits showed a statistical trend of being negatively correlated with each other. Although the correlative nature of the study does not permit a firm conclusion (Partridge & Harvey 1988; Bailey 1992), it is possible that the restraint hypothesis explains the relationship between reproductive performance and age in this goshawk population. Overall, the most likely explanation seems to be the constraint hypothesis, via age-related improvement, potentially of foraging skills, which has been favoured by other

authors as well (Sæther 1990; Forslund & Pärt 1995; Martin 1995; Laaksonen *et al.* 2002; Nielsen & Drachmann 2003).

One potential problem with this analysis is that the number of chicks fledged over the lifetime is not necessarily a very accurate estimate of fitness, i.e. the number of chicks recruiting into the breeding population (van Noordwijk & van Balen 1988). However, there is good evidence from passerines, seabirds, and notably birds of prey that number of chicks produced is highly positively correlated with number of recruits (Korpimäki 1992; Brommer *et al.* 1998; Weatherhead & Dufour 2000; Becker, Wendeln & Gonzalez-Solis 2001).

What about the mechanism causing the severe fitness consequences of early maturity in this goshawk population? The results indicate that the fitness consequences of early maturity are heterogeneous. There is strong evidence for selection to delay the age at first breeding (Fig. 3), but despite this many females started their breeding career aged 1. Incorporation of territory quality seems to solve this puzzle. Females starting to breed aged 1 only suffer a severe fitness consequence if they are in a bad-quality territory. Earlier results obtained from this goshawk population and other *Accipiter* hawks have indicated the marked influence of habitat heterogeneity as a factor influencing reproductive performance and even population growth rate (Newton 1991; Krüger & Stefener 2000; Krüger & Lindström 2001a). Given these profound fitness consequences of territory quality, why do females settle in bad-quality territories rather than delay breeding? Goshawks show a very high level of intraspecific aggression and fights over a territory are regularly fatal (Fischer 1983; Krüger & Stefener 1996). Given that a floating female will never be tolerated in an occupied territory (Fischer 1983), territory inspection is constrained. Models of dispersal commonly assume that birds assess a rather limited number of territories and settle in the best one they encounter (Lande 1987; Noon & McKelvey 1996; Ekman *et al.* 2001; Carrete *et al.* 2002). Given that good-quality territories are often occupied, assessing a small number of territories and choosing the best of those inspected will not guarantee occupying a good-quality territory. Hence, the pattern of territory availability might partly produce the fitness differences observed in this goshawk population. This mechanism can also explain the mismatch between the observed frequency distribution of age at first breeding (41.9% start breeding aged 1) and that predicted by the fitness analysis (optimal start of breeding aged 3, exhibited by only 13.5% of the females). Early breeding in a good-quality territory is favoured, but an early start in a bad-quality territory is strongly selected against.

Another, quite likely more important factor affecting this trade-off between territory quality and age at maturity is population density. This goshawk population has increased steadily from the lowest levels at the start of the 1980s over the last 25 years and the percentage of females entering the breeding population aged 1

has significantly decreased over this time period. With increasing density, the quality of available territories decreases significantly (Krüger & Lindström 2001a), which should select for later maturity, as was observed here.

In conclusion, this study has shown that a complex interplay between age-related changes in reproductive performance, habitat heterogeneity, and population density affect an important life-history trait: age at maturity, with important implications for fitness.

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