Impaired flight ability—a cost of reproduction in female blue tits

Cecilia Kullberg, David C. Houston, and Neil B. Metcalfe
Ornithology Group, Division of Environmental and Evolutionary Biology, IBLS, Graham Kerr Building, Glasgow University, Glasgow G12 8QQ, UK

When prey are attacked by predators, escape ability has an obvious influence on the probability of survival. Laboratory studies have suggested that flight performance of female birds might be affected by egg production. This is the first study of changes in take-off ability, and thus potentially in predation risk, during reproduction in wild birds. We trapped individual male and female blue tits repeatedly during the breeding season. Females were 14% heavier and flew 20% slower (probably as a consequence of a lower ratio of flight muscle to body mass) during the egg-laying period than after the eggs had hatched. However, flight muscle size did not change to compensate for changes in body mass over this period. In contrast, males showed no changes in either body mass, muscle size, or flight ability over the same period. Furthermore, the impairment of flight in females increased with the proportion of the clutch that had been laid, an effect that was independent of body mass and muscle size. This indicates that egg production causes additional physiological changes in the female body that produce impaired locomotor performance. We suggest that courtship feeding of female blue tits by their mates might reduce predation risk during the period when female take-off ability is impaired by reducing the time females have to spend foraging and thus reducing the time they are exposed to increased predation. Key words: blue tits, flight ability, Parus caeruleus, predation risk, reproduction. [Behav Ecol 13:575–579 (2002)]

Life-history theories suggest that present reproductive effort should be balanced between current fecundity and the probability of future survival and reproductive success. An increased predation risk during mate searching, copulation, and pregnancy, for example, is one factor that may reduce the future prospects of producing offspring (for a review, see Magnhagen, 1991). When prey are attacked by predators, the speed of escape has an obvious influence on the probability of survival. Reduced locomotor performance during reproduction has mainly been studied in reptiles, where gravid females of several species have been shown to experience a reduced sprint speed, which might result in an increased risk of predation (Bauwens and Thoen, 1981; Cooper et al., 1990; Siegel et al., 1987; but see also Qualls and Shine, 1997, 1998; Schwartzkopf and Shine, 1992). When small birds are attacked by predators, take-off velocity and flight maneuverability are crucial components in the likelihood of successful escape (e.g., Cresswell, 1993, 1996; Rudebeck, 1950). An increased body mass will increase wing load (body mass/wing area; see Pennycuick, 1989), which is likely to impair flight ability (Blem, 1976; Lima, 1986; Pennycuick, 1989).

Empirical studies suggest that birds face an increased predation risk due to impaired flight ability during migration (due to migratory fuel loads exceeding 20% of the birds’ lean body mass; Kullberg et al., 1996, 2000; Lind et al., 1999). Furthermore, experimental manipulation of body mass (both through adding artificial loads and by manipulating natural body mass) has shown effects on flight performance in starlings (Witter et al., 1994). Similar effects might be expected when breeding. During the reproductive season, female birds may increase in body mass by up to 30% due to the growth of gonads and eggs (Moreno, 1989). A study of sexual chases in sand martins showed that heavy females (due to natural and simulated egg loads) faced an impaired take-off ability compared to lighter birds (heavy females had about 30% longer time to ascending flight; Jones, 1986). Furthermore, in a study of flight ability in captive gravid starlings (Sturnus vulgaris), females reduced their angle of escape take-off by about 30% as a consequence of a 7% increase in body mass and a presumed change in the center of gravity of the body due to eggs and gonads (Lee et al., 1996). There is evidence for fast temporal changes in size of the pectoral muscle, the main flight muscle in birds; this might affect the power output during take-off and flight. An increase in pectoral muscle size in birds has been observed before migration and during molt, which probably is a compensation for the increased wing load (Biebach, 1998; Lind and Jakobsen, 2001; Piersma, 1998; Piersma and Lindström, 1997). There is no evidence that female birds increase their muscle mass to compensate for the increased wing load when carrying eggs. In fact, recent studies have shown that in many bird species, females instead face a reduction in pectoral muscle size during the egg-laying period (Houston et al., 1995c; Jones, 1990). It has been suggested, and shown experimentally in captive zebra finches (Taeniopygia guttata; Houston et al., 1995b), that this decline represents a direct contribution of muscle proteins to egg production (Houston et al., 1995a,b; Jones and Ward, 1976; Kendall et al., 1973). Furthermore, experimental increases in the physiological cost of egg production (increased clutch size) have been shown to reduce flight muscle condition in female zebra finches (Veasey et al., 2000, 2001) and lesser black-backed gulls (Larus fuscus; Magnnahan et al., 1998; Veasey et al., 2000, 2001). In captive zebra finches, this reduction in flight muscle size resulted in reduced flight ability after the completion of the clutch compared to the time before egg laying (Veasey et al., 2000, 2001). Thus, maternal predation risk due to reduced flight ability during reproduction might be important in the trade-off between reproductive effort and parental survival (Veasey et al., 2000).
Here we present the first empirical study of changes in flight ability, and thus potential change in predation risk, during reproduction in wild birds. Individual female and male blue tits (Parus caeruleus) were trapped at several occasions during reproduction, and their flight ability and body mass were recorded. To investigate whether there was any change in flight muscle size during the reproductive season, we also measured pectoral muscle size using a noninvasive method (Selman and Houston, 1996).

**METHODS**

We chose to study the blue tit because it is a mostly monogamous, hole-breeding, territorial passerine, which makes it relatively easy to trap both sexes repeatedly. Furthermore, female blue tits lay very large clutches (average about 11 eggs, ranging from 6 to 16; Cramp and Perrins, 1993), suggesting that the energy investment in the clutch might affect the physiology of the laying female. Indeed, the weight of a clutch is often heavier than the body mass of the laying female (Perrins, 1979). The female incubates alone, but the male feeds her during both egg laying and incubation, and both sexes feed the nestlings (Cramp and Perrins, 1995).

We studied the flight ability of wild, breeding blue tits in a population breeding in nest boxes in the mature oak woodlands surrounding the University Field Station, Rowardennan, Scotland (56°08’ N, 4°37’ W) in spring 2000. Pairs of blue tits were trapped with mist nets during the egg-laying period in the vicinity of their nest boxes. Immediately after trapping, we measured body mass (to the closest 0.1 g using a Pesola spring balance) and wing length (to the closest 0.5 mm) and ringed the birds. Each bird was then released at the base of a semitransparent, vertical, plastic tube to measure vertical take-off ability. At the top of the flight tube, there was a cage made of mist net where the bird could be collected after each flight (Figure 1). Each individual was released three times in the tube but was allowed to rest for at least 30 s between each flight. The flights were video recorded with a DVD video camera. Because the tube was semitransparent, the bird was visible through the plastic, and it was possible to analyze the video film and calculate the time it took the bird to cover a vertical distance of 140 cm. This measure was made by counting the number of video frames (each frame covering 0.02 s) between two marks on the tube at 20 cm and 160 cm height, respectively (Figure 1). There was no indication that the birds were decelerating by the time they passed the 160-cm mark (and, in fact, they often flew straight into the mist net roof of the collecting cage, suggesting that they did not detect it). To exclude flights that were not straight, or where the bird did not fly at its maximum speed, we used the fastest of the three flights as a measurement of the bird’s escape flight ability.

After the three flights, we measured the size of the pectoral muscle of the bird using a body mold in dental alginate (Cavex CA37 Superior Pink) (Selman and Houston, 1996), after which the bird was released. By cutting the mould dorsoventrally at the middle of the pectoral muscle, we obtained a measure of the cross-sectional area of the muscle, which was recorded by making five ink prints per mold on a paper. A horizontal line was drawn 5 mm perpendicular from the sternum keel of each print (5 mm was used as a standard measure because it is the average keel depth of a similar sized bird, the zebra finch; Selman and Houston, 1996). The enclosed area was then measured using the computer program Scion Image for Windows, Beta 4.0.2 (Scion Corporation), and an average area was calculated for the five prints from each mold (for a detailed description of the molding technique, see Veasey et al., 2000). A cross-section pectoral muscle area established with this molding technique has been shown to correlate with pectoral muscle lean dry mass in zebra finches (Selman and Houston, 1996). The mean cross-section pectoral muscle area is hereafter to be referred to as the muscle index. In dead animals in which muscles can be dissected, muscle ratio can be calculated as flight muscle mass per body mass (Marden, 1987); however, we calculated muscle ratio for the birds as muscle index per body mass.

In total we trapped 14 females and 12 males during the egg-laying period. When the chicks were 5 days old, we re-trapped 11 of the females and 6 of the males using nest-box traps. In addition, six of the females and one male were once again trapped when their chicks were 10 days old. Body mass, muscle index, and flight ability were measured on each trapping occasion. The work was performed under a bird-ringing license from the British Trust for Ornithology (no additional licenses were required). None of the blue tit pairs under study deserted their nests, and they were all successful in raising their broods to the age of fledging. We made statistical calculations using STATISTICA for Windows 5.5 (Statsoft Inc.). Results of Student’s paired *t* tests are presented unless otherwise noted.

**RESULTS**

The average clutch size of the studied blue tit pairs was 9 eggs (range 5–12). During egg laying, the females were significantly heavier, had lower muscle ratios, and flew slower than the males (body mass: $t_{22} = 8.1$, *p* < .0001, muscle ratio: $t_{19} = -4.8$, *p* = .00013; flight time: $t_{22} = 7.7$, *p* < .0001; Figure 2a). Male blue tits did not change in body mass, muscle index, or flight time from the period when their females laid eggs to the time when chicks were 5 days old (paired *t* test based
on males caught on both occasions; body mass: \( t_6 = 1.5, p = .2 \); muscle index: \( t_6 = 1.6, p = .2 \); flight time: \( t_6 = 1.6, p = .2 \); Figure 2). However, female blue tits lost an average of 14% of their body mass from egg laying to day 5 of chick rearing and another 3% from day 5 to day 10 of chick rearing (egg laying to day 5: \( t_{10} = 16.0, p < .0001 \); day 5 to day 10: \( t_{10} = 8.9, p < .0003 \), both comparisons are significant with sequential Bonferroni correction (Rice, 1988; Figure 2a). Because muscle index did not change in females during the investi-

gation (paired \( t \) test based on females caught on two occasions; egg laying to day 5: \( t_5 = -1.4, p = .2 \); day 5 to day 10: \( t_5 = 1.4, p = .2 \); mean \( \pm \) SE; egg laying: 0.83 ± 0.02 mm\(^2\); day 5: 0.85 ± 0.02 mm\(^2\); day 10: 0.81 ± 0.02 mm\(^2\)), their muscle ratios increased after egg laying (\( t_5 = -6.3, p < .0004 \)) to reach the same level as that of the males at day 5 of chick rearing (Figure 2b). There was no further change in female muscle ratio from early to late chick rearing (\( t_5 = 0.002, p = .9 \), Figure 2b). The increase in muscle ratio in females after egg laying was associated with a 20% decrease in flight time from egg laying to day 5, with no change in flight ability from early to late chick rearing (egg laying to day 5: \( t_5 = 8.10, p < .0001 \); day 5 to day 10: \( t_5 = -1.9, p = .12 \); Figure 2c). Thus, when the chicks were 5 days old, there were no differences in body mass, muscle index, muscle ratio, or flight time between the sexes (body mass: \( t_{20} = 1.0, p = .4 \); muscle index: \( t_{20} = 1.7 \), females, \( n = 12 \), males, \( n = 10 \), \( p = .1 \); muscle ratio: \( t_{12} = 2.0, p = .06 \); flight time: \( t_{12} = 0.12, p = .9 \); Figure 2). During the egg-laying period, the females had laid between 1 and 11 eggs at the time that they were caught, representing 20–90% of their final clutch size. Neither the percentage of the final clutch already laid when trapped nor the absolute number of eggs laid correlated with either the body mass or muscle index of the females (linear regressions with body mass as the dependent variable: effect of percentage of clutch laid: \( n = 14, r^2 = .02, \beta = -0.15, p = .6 \); effect of absolute number of eggs laid: \( n = 14, r^2 = .005, \beta = -0.07, p = .8 \); muscle index as the dependent variable: effect of percentage of clutch laid: \( n = 11, r^2 = .01, \beta = -0.11, p = .9 \); absolute number of eggs laid: \( n = 11, r^2 = .03, \beta = -0.03, p = .9 \)). However, females that had laid a larger proportion of the clutch flew slower than females trapped at the beginning of their egg-laying period, and percentage of final clutch already laid was a better predictor of flight performance than the absolute number of eggs laid (linear regression: percentage of clutch laid: \( n = 13, r^2 = .43, \beta = 0.65, p = .015 \); Figure 3; absolute number of eggs laid: \( n = 13, r^2 = .39, \beta = 0.62, p = .02 \)).

**DISCUSSION**

There was a dramatic change in the flight ability of female blue tits during the breeding season. Females had a markedly lower vertical flight speed during egg laying than after the
eggs had hatched, when they flew just as fast as the males. The fact that the flight performance of males did not change during reproduction indicates that there was no habituation effect on flight speed due to repeated flight trials, nor any overall seasonal effects.

Female blue tits lost 14% of their body mass from egg laying to day 5 after hatching, but their muscle size did not change. This compares with a 25% decrease in body mass over approximately the same period recorded from southern England when female blue tits were dissected during different stages of the breeding cycle (Woodburn and Perrins, 1997). The reduction in body mass observed in the dissected females was mainly due to the absence of eggs and reduction in sex organs and water content in the body (19% of body mass at laying), and there was no difference in pectoral muscle mass between these two periods. The smaller decrease in body mass in females in our study compared to the study in southern England is mainly due to a lower body mass during egg laying, which might be related to the smaller clutch size in our study area (average 9 eggs compared to 11 eggs in southern England; Cramp and Perrins, 1993). The loss of body mass after laying led to an increase in muscle ratio, which was associated with a 20% improvement in take-off speed in the female blue tits. However, the relatively smaller reduction in body mass from day 5 to day 10 of nesting development did not affect the flight ability of the parental females.

In a previous study of flight ability in captive starlings, females were found to maintain flight speed but take off at a shallower angle when gravid (Lee et al., 1996). However, the starlings were free to adopt any escape angle, whereas in our experimental setup blue tits were forced to take off vertically, which is probably the most power-demanding maneuver for a bird. Thus, as suggested by Lee et al. (1996), females probably reduce take-off angle to defend velocity when possible.

If an increased body mass (and an eventual change in the center of gravity of the body) was the only factor reducing flight ability in female birds during egg laying, we would expect flight ability to remain stable during the course of the laying period because body mass does not change in female blue tits during this period (Woodburn and Perrins, 1997). However, female blue tits flew slower the later in their laying cycle that they were trapped, even though muscle index and body mass did not differ. This suggests that egg laying produces a cumulative cost to flight performance other than that caused by mass change. Female zebra finches that were manipulated to lay larger clutch sizes (by experimentally removing eggs from the nest when laid, which induced the female to continue laying) exhibited a reduction in flight ability over the egg-laying period (Veasey et al., 2000, 2001). However, in zebra finches this reduction in flight ability was coupled with a reduction in flight muscle size (Veasey et al., 2000, 2001). Zebra finches have been shown to use stored muscle protein for the production of eggs, which is probably an adaptation to their low-protein diet (Houston et al., 1995a). In contrast, blue tits, like most small passerines, feed on more protein-rich food and have thus been assumed to accumulate energy and nutrients on a more or less daily basis for egg production (Meijer and Drent, 1999; Perrins, 1996; Woodburn and Perrins, 1997). Our results suggest that this may not be the full story because the reduction in locomotor ability during the course of laying was independent of muscle condition or body mass; more detailed physiological studies of the body of laying females are therefore required to determine the causes of this decline in performance. A physiological effect on locomotor performance during gestation has been suggested for a viviparous lizard because running speed was unrelated to litter mass and did not increase after parturition (Olsson et al., 2000). However, a direct comparison with passerine birds is hard because the lizard studied has a gestation period of 15 months.

Our results indicate that female blue tits experience an increased risk of predation during the egg-laying period. In accordance, Dobson (1987) found that female blue tit mortality peaks during egg laying and incubation, whereas male mortality peaks earlier in the breeding season when territories are established. However, data on mortality rates in the study were based on ring recoveries, and they probably underestimated mortality due to raptor predation. There are relatively few studies of predation rates of birds during the breeding season (Lima and Dill, 1990), and even fewer quantifying differences between the sexes. Female-sketched mortality due to goshawk (Accipiter gentilis) predation during the early stages of breeding has been shown in black grouse (Tetrao tetrix; Angelstam, 1984) and capercaillie (Tetrao urogallus; Widén, 1987). Furthermore, detailed studies of prey choice of sparrowhawks (Accipiter nisus) based on feather remains at nests has shown that breeding female chaffinches (Fringilla coelebs; Götmark et al., 1997) and blackbirds (Turdus merula; Post P, unpublished data) face a significantly higher predation rate from sparrowhawks than do males (despite the females being more cryptically colored). Because male chaffinches do not provide females with food and do not incubate the eggs, the high energy demand of female chaffinches during egg laying and incubation forces them to spend more time foraging than males (Götmark et al., 1997). Intense foraging will reduce the time available for predator vigilance, and this in combination with a reduced take-off ability once attacked might explain the observed high predation rate in breeding females. In blue tits, the male provides his mate with food during egg laying and incubation, to the extent that this courtship feeding can cover her daily energy requirements for egg production (Krebs, 1970). As suggested by Lee et al. (1996), courtship feeding might not only contribute extra protein for egg production and restoration of depleted body reserves in the female, but also reduce her predation risk during the period that she has an impaired take-off ability by reducing the time she has to spend foraging and thus exposing herself to raptor attacks.

We thank Caroline Askew and Sven Jakobsson for invaluable assistance in the field, Jan-Åke Nilsson for practical advice, and Richard Shine for comments on the manuscript. This work was supported by a Fellowship from the Swedish Natural Science Research Council (to C.K.).

REFERENCES


