Articles

Body mass variations in disturbed mallards *Anas platyrhynchos* fit to the mass-dependent starvation-predation risk trade-off

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For passerines the starvation-predation risk theory predicts that birds should decrease their body mass to improve escape flight performance, when predation pressure increases. To investigate whether this theory may apply to large birds, which manage body reserves differently from small passerines, we experimentally increased the predation risk in mallards *Anas platyrhynchos*. Two groups were disturbed at different frequencies during experimental sessions lasting one week, while a control group was left undisturbed. We found that body mass loss and final wing loading were similar in both disturbed groups and significantly differed from the control group. Food intake in disturbed groups was reduced up to day four of the disturbance session and was lower than in the control group. Altogether our results suggest that disturbed mallards may adjust their body mass to reach a more favorable wing loading, supposedly to improve escape flight performance. Nevertheless, body mass loss in our mallards was double than what has been observed in passerines. This greater mass decrease might be explained by different strategies concerning energy storage. Furthermore, in large birds the predation component of the starvation-predation trade-off might be of greater importance. Hence, the observed relevance of this trade-off over a large size range suggests that the starvation-predation risk theory is of major ecological significance for many animal species.

Survival of wild birds depends on how they cope with changes in their abiotic environment, such as food availability and seasonal climate changes, but also how they manage biotic risks, like predation (Lima 1986, Witter and Cuthill 1993). In avian species, predation was considered as one of the most important selective pressure in the evolution of morphology and behavior (Lima 1998, Veasey et al. 1998). It has been proposed that predation risk was mass-dependent in the context of the starvation-predation risk trade-off (Lima 1986, Witter and Cuthill 1993, Witter et al. 1994), which is a key challenge for individual fitness (MacLeod 2006, MacLeod and Gosler 2006, MacLeod et al. 2007a). Suggested benefits of high body mass associated to fat storage include body insulation, mechanical support, protection, buoyancy together with sexual and social signals (Pond 1978). Nevertheless, the most general and admitted benefit of fat storage is that lipids are the major energy reserves (Grimminger 1976). Indeed, birds have high metabolic rate and body temperature and use flapping flight which is the most energetically requiring mode of locomotion per unit time (Witter and Cuthill 1993).

Despite sufficient body reserves have to be kept in anticipation of unpredictable fluctuations in food availability, it has been also shown that fat storage has mass-dependent costs linked to energy expenditure and predation risk (Lima 1986, McNamara and Houston 1990,

Witter and Cuthill 1993). In fact, the mass-dependent predation risk hypothesis predicts that body mass should be maintained as low as possible (Lima 1986, Houston and McNamara 1993, Houston et al. 1993). Carrying large body reserves increases predation exposure due to the greater foraging time required and/or to greater metabolic demands (McNamara and Houston 1990, Witter and Cuthill 1993, Bednekoff and Houston 1994, Brodin 2001). Moreover, it impairs flight maneuverability (Witter and Cuthill 1993, Witter et al. 1994). Actually, an enhanced body mass is also associated with a higher wing loading and, therefore, with greater energetic costs of transport. Moreover, despite controversial results in some studies (Kullberg 1998, Kullberg et al. 1998, Veasey et al. 1998, van der Veen and Sivars 2000), it has been shown among several species that a higher body mass impairs take-off performances through a smaller ascent angle or a lower speed (Witter et al. 1994, Metcalfe and Ure 1995, Kullberg et al. 2005, MacLeod 2006). In fact, different organ groups may contribute to body mass adjustments to improve flight capabilities. The reduction of the digestive tract mass has been shown to lower the energetic cost of flight (Piersma and Lindström 1997). Moreover, pectoral muscle size in ruddy turnstones *Arenaria interpres* increases independently of unchanged body mass in response to an increase in predation risk (van den Hout et al. 2006). Conversely, red

knots *Calidris canutus* respond to predation risk increase by decreasing body mass, whilst the pectoral muscle mass remains unchanged (van den Hout et al. 2010). This difference in response is probably linked to specific escape strategies in both species. Ruddy turnstones are vulnerable to surprise attacks by raptors and they rely on speed based escape requiring high pectoral muscle power output. Red knots forage in open environments and detect predators early, so they rely on collective flight and maneuvers to escape, implying large turning maneuverability linked to low body mass (van den Hout et al. 2010).

A significant support for this mass-dependent starvation-predation risk trade-off has only come from studies on small passerines species (MacLeod et al. 2007a). These studies show that body mass is regulated on a daily basis, according to predation risk (Gosler et al. 1995, Lilliendahl 1997, Cresswell 1998, Gentle and Gosler 2001, Kullberg et al. 2005, MacLeod et al. 2005a, b, MacLeod 2006). Field observations have shown that the body mass of British great tits *Parus major* increases in years when the density of their main predator, the sparrowhawk *Accipiter nisus*, is low, while the reverse is true in years of high predator abundance (Gosler et al. 1995). Additionally, experimental studies have shown that when the perception of predation vulnerability increases or when birds are chased, food consumption is regulated in order to decrease body mass (Lilliendahl 1997, Carrascal and Polo 1999, Gentle and Gosler 2001). Such adjustments should maximize survival, since escape take-offs should be performed at a maximum power output, which increases with a decrease in body mass (Pennycuick 1989). Conversely, some studies found an increase in body mass in response to the presence of predators (Fransson and Weber 1997, Lilliendahl 1998, Pravosudov and Grubb 1998, MacLeod et al. 2007b). Those results are in accordance with predictions of the interrupted foraging model in which birds gain mass in the presence of predator due to the uncertainty of getting food (McNamara et al. 1994, MacLeod et al. 2007b).

Dealing with this question of body mass variations under increased predation risk is strongly lacking among larger bird species that have to match several changes in environmental pressure during their annual cycle. Especially, non-passerine birds with a higher body mass manage their body reserves differently from passerine species, with little daily, but important seasonal mass changes (Haftorn 1989, Blem 1990, Loesch et al. 1992). Thus, one can hypothesize that, particularly during the wintering period, the starvation component of the starvation-predation risk trade-off should likely be regulated differently in larger birds when compared with passerines. Because larger species are less sensitive to starvation, they could show a larger proportional reduction in their body mass in response to increased predation pressure. Additionally, assuming that the ratio between the power available and the power required to fly (power margin) is lower in larger birds than in passerine birds (Norberg 1996), we can hypothesize that in larger species body mass variations should affect flight performance and, hence, escape chances from a predator more strongly than in small birds.

To give a further insight about the question of body mass changes under high risk situation we artificially increased predation risk in mallards *Anas platyrhynchos*.

This species is one of the most numerous and widespread duck species in the Northern hemisphere and lives in shallow waters, on marshes and on the ground (Owen and Black 1990, Del Hoyo et al. 1992). Thus, individuals can be attacked by terrestrial predators like red foxes *Vulpes vulpes*, or mink *Mustella vison* (Sargeant et al. 1973, Sargeant et al. 1984), but also by raptors like marsh harriers *Circus aeruginosus*, gyrfalcons *Falco rusticolus*, bald eagles *Haliateetus leucocephalus*, or by the Caspian gull *Larus cachinnans* (Tamisier and Dehorter 1999, Fritz et al. 2000, Dekker and Court 2003). In response to these attacks mallards can dive but, most often they fly away to reach a cover (high vegetation), or another pond (Tamisier and Dehorter 1999, Fritz et al. 2000, Dekker and Court 2003). Moreover mallards, among the larger ducks (with a body mass 7 to 100 times higher than that of passerines), have one of the highest wing loading to body mass ratio in birds and a very low power margin (Norberg 1996). This species is therefore of particular interest for investigating the response in body mass change to an increased predation risk associated to disturbance.

Methods

Animals and experimental conditions

The study was conducted on three groups of 14 mallards originating from the registered rearing centre of "la Canarderie de la Ronde" (Cère la Ronde/France). Each group (7 females and 7 males) was maintained in an outdoor tunnel-aviary of 100 m^2 (20 by 5 m) with a height of 2.5 m and was subjected to ambient temperature and natural photoperiod. The aviaries, close to the laboratory, were protected against predators by an electric fence. Tunnels contained a 4 m^2 pool (0.60 m depth), supplied with running water, that was situated at the same location in each tunnel, so that configuration was identical for all groups. A balanced commercial diet (Standard duck food 7751, Sanders Co) was provided *ad libitum* in feeders placed on 2 by 2 m covers, to account for food spillage. The acclimation period to experimental conditions lasted one month (September 2006).

Experimental procedure

Disturbance
We experimentally increased the perceived predation risk of mallards by increasing human disturbance that triggers animal's responses typically evolved against natural predators (Frid and Dill 2002). Two groups were disturbed during three sessions lasting one week each, separated by about 1.5 months. Group 1 (G1) was disturbed twice daily for 15 min (between 08.00 and 11.00 hours) for one week. These sessions began on 30 Sept. 2006, 22 Nov. 2006, and 4 Jan. 2007. Group 2 (G2) was disturbed four times daily for 20 min periods (between 08.00 and 11.00 hours). Sessions for G2 started on the day after the G1 sessions ended. The third group was not disturbed and was used as the control group (CG). The disturbance was provoked by a radio-controlled toy car (E-Zilla FWD Hot-boddies™) that was steered with high speed towards the ducks, until

they took off. After take-off, we waited until they had settled, then we gathered them together with the car and made them take-off again. We repeated this procedure for 15 and 20 consecutive minutes in G1 and G2, respectively. Preliminary tests showed that this procedure was the most efficient in inducing simultaneous take-off of all birds in the group. No ducks were hurt during these trials. During disturbance periods, two experimenters (CZ, MB) were near the aviaries to pilot the radio-controlled car and to quantify the number of take-offs. The aviaries, distant from each other by 10–15 m, were separated by opaque barriers. Moreover we checked that to disturb birds in a given group did not change the behavior of ducks in the other groups (self-maintenance or alert behavior). We placed night-view cameras in front of each tunnel to ensure that any other disturbances outside the disturbance periods would not go unnoticed. This work was performed under the governmental authorizations to conduct experiments on animals Numbers 67-99 and 67-285 and was approved by the Dept. Veterinary Services. The experiment complied with the "Principles of Animal Care" publication No. 86-23, revised 1985 of the National Institute of Health, and with current legislation (L87-848) on animal experimentation in France.

Weighing and wing loading

Ducks of the disturbed groups were caught with a net and weighed ($\pm$ 0.1 g) in a nearby room one day before the beginning of each disturbance session, four days after its start, and on the last day, immediately after the last disturbance period. Control animals were weighed at the same frequency as disturbed groups. The birds of each group were released together in their respective aviary after weighing.

The wing area of the birds was determined from the outline of the stretched right wing, first drawn onto paper and then digitized using Sigma-Scan software (version 3.9). Total wing area was taken as double the right wing area. Wing loading (g.cm^{-2}) was determined by dividing body mass by total wing area.

Food intake

Daily food intake measurements began one week before each disturbance session and ended one week after its completion. Each day at 18.00 h, 2 kg of fresh food was given to the birds, while the food remaining from the preceding 24 h was removed. Food spilled on the covers was also collected. To avoid water content modifications, all food given to the birds and removed from the feeders was dried for 24 h at 40 °C in an oven, before being weighed.

Statistical analysis

Two-way and three-way ANOVA's were used to test for differences between sessions, groups and sexes. Within the same group and the same sex, differences in body mass and wing loading were tested with an ANOVA for repeated measures. Holm-Sidak test was used as a post-hoc test following all ANOVAs after checking for normality and homogeneity of variance (Sigmastat 3.0, SPSS). When normality and homogeneity of variance failed, Friedman for repeated measures or Kruskal Wallis non-parametric tests were conducted. Student's t-test was used when comparing two groups. Least squares correlations were conducted using Sigma plot SPSS (11.0). All statistical tests were two-tailed, and probability levels < 0.05 were considered as significant. Means values provided are given $\pm$ SE.

Results

On average, birds of G2 (the stronger disturbed group) performed nearly twice as many take-offs than those of G1 (the less disturbed group) ($F_{1,83} = 408.9$, $p < 0.001$; Fig. 1a). For each group, there was no difference between sexes ($F_{1,41} < 0.53$, $p > 0.45$; Fig. 1a). The number of daily take-offs did not differ between all sessions in G1 and in G2 ($F_{2,83} < 2.13$, $p = 0.13$).

For each sex in both disturbed groups body mass loss, final and initial wing loading were not significantly different between sessions ($F_{2,83} < 1.62$, $p > 0.21$). For males and females, body mass loss was significantly higher in G1 and G2 (between 8 and 11% in females and between 6 and 7% in males) than in the CG ($t > 5.86$, DF $= 40$, $p < 0.001$; Fig. 2). In the control group the body mass decrease (2%) was not significant ($p > 0.18$) in any of the sessions. Final
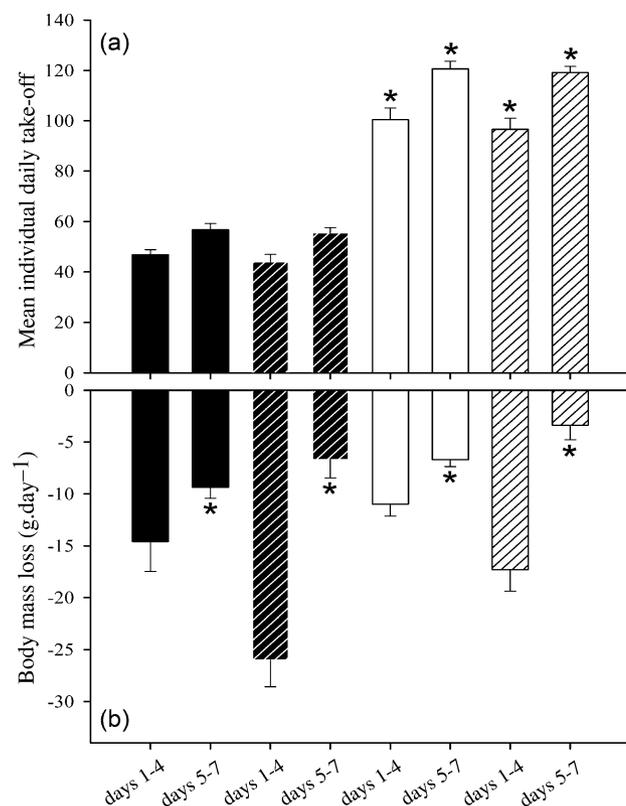

Figure 1. Number of daily take-offs (a), and body mass decrease (g.day^{-1}) (b) averaged for the three disturbance sessions. Values are means $\pm$ SE. Males of group 1 (G1) and group 2 (G2) are indicated in black and white, respectively, while females of G1 and G2 are indicated in hatched black and hatched white, respectively. (a) *: G2 significantly different from G1 ($p < 0.001$). (b) *: days 5–7 significantly different from days 1–4 ($p < 0.05$).
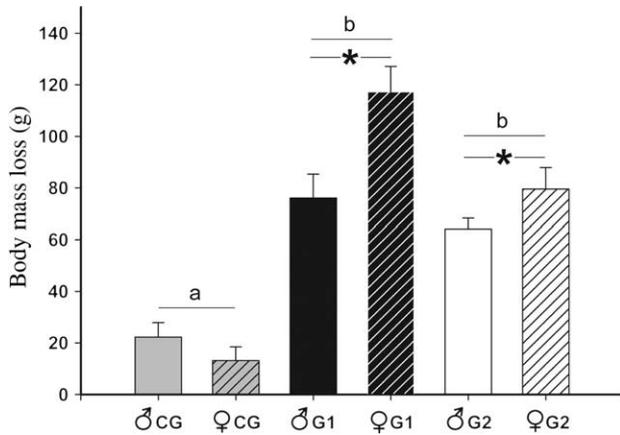
Figure 2. Mean body mass loss over the three sessions for each sex of the three groups. Values are means ± SE. Males of CG, G1 and G2 are indicated by grey, black and white bars respectively, while females of CG, G1 and G2 are indicated in hatched grey, black and white bars respectively. Letters specify differences between the three groups. * specify significant differences between sexes within groups.
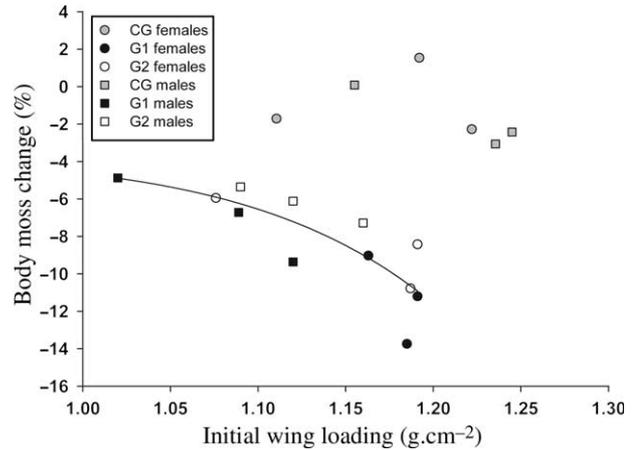

Figure 3. Relationship between body mass loss during three disturbance sessions and initial wing loading (values given are means). CG females are indicated by grey circles, and G1 and G2 females by black and white circles, respectively. CG males are indicated by grey squares and males of G1 and G2 by black and white squares, respectively. The relationship in disturbed groups is best described by $y = -0.9 \, x^{11.85} - 3.75$, $R^2 = 0.67$, $F = 9.01$, $p = 0.007$ and indicates that body mass loss was greater, when the initial wing loading was higher. There is no significant relation in the control group ($p > 0.13$).

Discussion

We show here that disturbed mallards reduced their food consumption and body mass. As a result their power margin for flight increased and we suggest that it may improve their escape performances. The amplitude of these adjustments was independent of the disturbance intensity but unequivocally related to the pre-disturbance wing loading.

In this experiment, the body mass decrease of the two disturbed mallard groups was three to six times higher than

wing loading at the end of the disturbance sessions was lower (t > 2.82, DF = 40, p < 0.05) in G1 and G2 birds (between 0.99 and 1.06 $g.cm^{-2}$) than in CG birds (1.17), although initial wing loading did not differ between groups (t < 1.16, DF = 40, p > 0.82).

Body mass loss and final wing loading were similar for G1 and G2 during all disturbance sessions ($F_{1,41} < 3.10$, p > 0.12). In the disturbed groups, mean daily body mass loss was higher during the first four days of disturbance than during the three following days ($F_{1,41} > 6.0$, p < 0.05; Fig. 1b). However, there was an exception for males of G1 during session 2, for which there was no difference (t = 1.21, DF = 40, p = 0.10). Although final wing loading was not different between sexes ($F_{1,83} = 0.58$, p = 0.45), body mass loss and initial wing loading were higher in females than in males for both disturbed groups and during all sessions ($F_{1,83} > 5.98$, p < 0.02; Fig. 2). Final wing loading was not related to body mass loss ($R^2 = 0.08$, $F_{2,11} = 0.56$, p = 0.47) but initial wing loading was. When initial wing loading was higher, body mass loss was greater ($R^2 = 0.67$, $F_{2,11} = 9.01$, p = 0.007, Fig. 3). Moreover, initial wing loading was not related to body mass loss in the control group ($F_{2,5} < 4.33$, p > 0.13; Fig. 3).

When compared with the mean value recorded before disturbance (pre-D), daily food consumption during disturbance sessions differed between the control group and both disturbed groups ($F_{1,80} > 13.15$, p < 0.001), while it did not differ between the disturbed groups ($F_{1,59} = 1.06$, p = 0.31; Fig. 4). In G1 and G2, between day 1 and 4 of disturbance, food intake decreased between 40 and 47%, respectively (ANOVA post hoc test, p < 0.05), when compared with the initial value and differed significantly (t > 2.45, df = 10, p < 0.05) from that of control birds. After day 4 of disturbance, food intake increased in the disturbed groups and from day 5 of disturbance, it did not differ from the initial values (ANOVA post hoc test, p > 0.05).
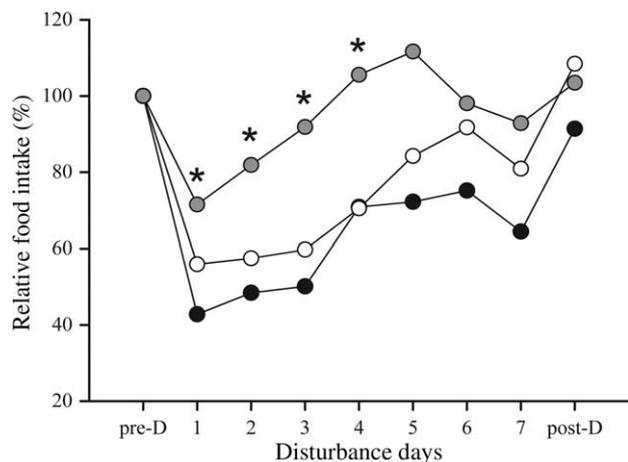

Figure 4. Food intake (means) during three disturbance sessions and during the week following disturbance (post-D). Values are expressed in relation to the mean food intake before disturbance (pre-D, taken as 100%). G1 and G2 are indicated by black and white circles, respectively, while the control group (CG) is indicated by grey circles. *: CG significantly differed from both disturbed groups for a given day (p < 0.05).

in the control group. The limited body mass loss we observed in the control group was likely caused by handling stress (Lilliendahl 1997, van der Veen and Sivars 2000, MacLeod and Gosler 2006). The higher body mass loss in the disturbed groups rather resulted from mass-dependent costs associated with the disturbance. Actually, the body mass loss of birds was not related to the intensity of the disturbance or the frequency of take-offs (escape flights). Yet, energy expenditure during these short flights should be at least three times higher than during sustained flapping flights (Nudds and Bryant 2000, Videler 2005). If body mass loss would be explained by increased energetic costs associated with the increased number of escape flights in disturbed birds, one would expect that birds of G2 should have lost more mass than those of G1. Since this was not the case, we propose that the extent of body mass loss in mallards was not primarily the result of an increased energy expenditure caused by the greater number of escape flights during disturbance. While sufficient energy stores are maintained such a strategy has an advantage since it may reduce exposure to predators and may improve escape flight performance. Indeed, it is proposed that a decrease in body mass results in a reduction of the energetic maintenance costs, foraging time, and wing loading (Houston and McNamara 1993, Houston et al. 1993, Bednekoff and Houston 1994, Witter et al. 1994, Brodin 2001). Our findings are therefore consistent with the prediction of the starvation-predation risk trade-off theory (Lima 1986, Houston et al. 1993, Witter and Cuthill 1993). Hence, it may allow extending this theory to birds with higher body masses than passerines although having a different strategy in managing body reserves and a different ecology.

In response to disturbance birds decreased their food intake, although food was provided *ad libitum* (Fig. 4). Food intake of disturbed birds was lower than in control birds but only between day one and four of each disturbance session. Moreover, for each session, mass loss was fast during the first four days and slowed down afterward. Consequently, we think that the increase of food intake after the day four did not result from an habituation to the disturbance but was rather associated to body mass loss that become lower from this day. Furthermore, astonishingly we found no difference in food intake between the two disturbed groups, despite the fact disturbance level in G2 was twice as high as in G1. Thus, mallards did not compensate for the higher immediate energy expenditure resulting from the induced escape flights by increasing their energy intake. Foraging in mallards typically occurs throughout the day and usually accounts for less than 35% of their time budget (Jorde et al. 1984). Since the maximum disturbance duration in our study was 80 minutes (i.e. 5% of the time budget) and occurred only during daytime, the disturbed mallards were not limited by the time potentially available for foraging. Hence, models of interrupted foraging (McNamara et al. 1994), which state that birds might gain weight because of a reduced probability to access food when disturbed, are not adequate in explaining the present observed response. According to Lilliendahl (1997) and Carrascal and Polo (1999), we can therefore propose that the mechanism for the weight loss observed in our study rather resulted from an adjustment through a lowered food intake. Moreover, it has been

suggested that birds might reduce the mass of some digestive compartments as an anticipatory mechanism to reduce the energetic costs of locomotion (Piersma and Lindström 1997). However, the decrease in body mass we observed was unlikely to result exclusively from the diminution of the digestive compartment. Thus, in long term fasted mallards (up to the end of phase II, see Robin et al. 1991 for details) the maximal decrease in body mass explained by a reduction of this compartment (organs plus digestive tract content) was about 40 g (i.e. 4% of body mass; Robin et al. 1991, Boos et al. 2007). The body mass reduction we observed in the disturbed groups was far greater and, in our experiments, the food intake was only partly reduced and birds were never fasted. This implies that other body compartments must have been affected. The mass loss we observed in both disturbed groups was higher in females than in males. Actually among mallards, females are known to have a higher fat/protein ratio than males (Boos et al. 2002). Hence, the body mass decline we observed may have affected body lipid amounts and muscle mass differently between sexes. It therefore would be relevant in this context, to investigate how disturbances might affect the actual body composition of birds and, in the long term, future reproductive success. In this context, it would be valuable to examine pectoral muscle size variation since its changes could be decoupled from body mass variations (van den Hout et al. 2006). According to the flocking behavior and gregarious ecology of mallards, we can assume, as in red knots (van den Hout et al. 2010), that pectoral muscle size should remain unchanged. Further studies are obviously needed to answer these questions.

Wing loading, which correlates negatively with flight speed, is a key variable in determining flight performance (Norberg 1996). High wing loading might impair the escape ability during predator attack by decreasing the take-off angle and aerial maneuverability (Witter et al. 1994, MacLeod 2006). Although the final wing loading we measured was not related to body mass loss, we found that body mass loss was greater when initial wing loading was high in all sessions. Furthermore, although initial wing loading values were different between sexes, final wing loading of each session in the two disturbed groups was similar for both sexes and lower than in the control group. Altogether, those results suggest that mallards adjusted their body mass to reach a more favorable wing loading that may enhance take-off speed and maneuverability at a low energetically cost and, thus, should improve escape performance during predator attack. This idea receives further support from the fact that body mass decline was not linear. This was concomitant with an increase in food intake after day four. These results suggest that mallards adaptively and spontaneously adjusted their body mass by controlling the amount of food intake in response to disturbance, regardless of its intensity. Importantly, our data underscore that body mass loss would be balanced according to the required mechanical power for flight and the need to maintain sufficient body fuels. Our results lend support to the fit-for-flight hypothesis, which predicts that mass is lost adaptively to prepare for predator escape (van der Veen and Sivars 2000). They are also in agreement with the starvation-predation risk trade-off (Lima 1986, McNamara and Houston 1990). Although the wing loading reduction

through body mass loss that we observed appears to be adaptive, we cannot conclude as yet that it is really an adaptation, i.e. that this trait was selected for its effect on predator avoidance. In fact, the increase in predation risk can also lead to behavioral changes (Lima and Dill 1990, Lima 1998). One can suppose that vigilance behavior might be increased in disturbed ducks, which could have led to the observed decrease of food intake. Additionally, ducks can use unihemispheric slow-wave sleep (USWS) when perceived risk increases. During USWS one hemisphere sleeps whereas the other remains awake with the contra-lateral open to allow predator detection (Rattenborg et al. 1999a, b). These behavioral modifications may possibly increase energy expenditure and lead to body mass loss. Nevertheless, it has been shown that although disturbance in fast-living species does not increase mean daily energy expenditure, it could be different for slow-living species (Bisson et al. 2009). In our case, it appears that the observed body mass loss was not primarily due to an increase in energy expenditure because the global response was the same in both disturbed group, despite the fact that G2 was disturbed twice as much as G1 (see above). This underlines the fact that body mass loss seems to be an adaptive response to the increase in predation rather than a by-product of other processes. Nevertheless, directly measuring energy expenditure of the ducks in response to disturbance would better support this conclusion. It would be also relevant to study the associated behavioral adjustments. We intend to address these questions in greater details elsewhere to better appreciate whether or not the body mass loss we observed can be considered as an adaptation.

Several theoretical models related to the mass-dependent predation risk hypothesis have been developed for birds but they only received empirical support from studies on passerines, such as tits (Gosler et al. 1995, Carrascal and Polo 1999, Gentle and Gosler 2001, MacLeod et al. 2005a), greenfinches (Lilliendahl 1997) and blackbirds (Cresswell 1998, MacLeod et al. 2005b), with a body mass range between 10 and 150 g. Our study gives a new insight of this theory among larger birds such as mallards which are particularly exposed to predation and more generally to disturbance. Interestingly, we show in this species that the relative body mass loss associated with an increased predation risk was about twice as much as in small birds (6–11% *vs* 2–5%; Gosler et al. 1995, Lilliendahl 1997, Carrascal and Polo 1999). Differences in the strategy of body reserve storage might explain this differential adjustment in body mass decrease between passerines and ducks. In the former, fat reserves built up during the day are burnt for energetic purposes during the following night (Haftorn 1989, Blem 1990). Consequently, the daily mass variation cycle, with a diurnal increase of about 7–12%, is of greater amplitude than the winter fattening cycle (body mass variation: 2 to 8%; Haftorn 1989). By contrast, mallard ducks usually store larger body reserves than required to cope with common periods of several days cold spells. Thus, body mass changes are larger in this species (5 to 20%; Pattenden and Boag 1989, Loesch et al. 1992, Boos et al. 2007) than in passerines during the winter fattening cycle. Subsequently, we suggest that large birds can sustain a higher body mass (and body reserves)

reduction in response to increased predation pressure than small birds, without adversely impairing their capacity to endure starvation as it would be the case in passerines. Additionally, in large avian species, especially ducks, which are among those having the highest wing-loading (Norberg 1996), such an adjustment could have important consequences for the power margin ratio (power available/ power required). This ratio is important to characterize flight performance and is known to decrease as the body mass of a given species increases (Norberg 1996). In passerines, a body mass reduction of 2–5% in response to increased predation pressure would correspond to a 0.3–0.8% gain in power margin (calculated from Gosler et al. 1995, Lilliendahl 1997, Carrascal and Polo 1999). In mallards, reduction in body mass was twice as great (6–11%) and would correspond to a 4 to 10 times greater gain in power margin (4.5%), compared to passerines. Consequently, we suggest that the extent of the response to the starvation-predation risk trade-off is not solely species-specific but rather directly related to the size of the species.

To conclude, in this experimental study, we demonstrated that mallards seemed strategically to lose body mass, likely in an attempt to achieve a more favorable wing loading. The relationship between body mass loss and power margin we found for mallards is different from what has been reported for passerine species, most likely because of different size constraints. Considering the fundamental nature of the starvation-predation risk trade-off, we suggest that this size-dependent adjustment should be applicable to many animal species (not only birds), as it has also been suggested by a recent study on harbor porpoises *Phocoena phocoena* (MacLeod et al. 2007a). Hence, the relevance of the mass-dependent predation risk hypothesis for animals of a wide size range (including birds and mammals) suggests that mass-dependent behavior is of great, not yet fully acknowledged, ecological significance for many animal species, regardless of size and habitat (MacLeod et al. 2007a). The significance of this idea should be better taken into account when addressing the conservation of animal populations.

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