Water bathing alters the speed-accuracy trade-off of escape flights in European starlings

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Birds of most species regularly bathe in water, but the function of this behaviour is unknown. We tested the hypothesis that water bathing is important in feather maintenance, and hence should enhance flight performance. We manipulated European starlings', *Sturnus vulgaris*, access to bathing water in a 2 x 2 design: birds were housed in aviaries either with or without water baths for a minimum of 3 days (long-term access) before being caught and placed in individual cages either with or without water baths for a further 24h (short-term access). We subsequently assessed the speed and accuracy of escape flights through an obstacle course of vertical strings. Birds that had bathed in the short term flew more slowly and hit fewer strings than birds that were deprived of bathing water in the short term, whereas long-term access to bathing water had no significant effect on flight performance. Thus recent access to bathing water alters flight performance by altering the trade-off between escape flight speed and accuracy. We hypothesise that lack of bathing water provision could increase anxiety in captive starlings because of an increase in their perceived vulnerability to predation. This study therefore potentially provides an important functional link between the expression of natural behaviours in captivity and welfare considerations.

Keywords:
animal welfare;
dustbathing;
European starling;
manoeuvrability;
passerine;

Sturnus vulgaris;
water bathing.

Maintenance behaviour has received very little attention from behavioural biologists, despite forming a significant part of the time budgets of many animals. For example, a comparative study by Cotgreave & Clayton (1994) found that, across 62 bird species, individuals spent an average of 9.2% of the day in maintenance behaviours (range 0.3-25.4%). An important element of avian maintenance behaviour involves bathing in water. Birds of the majority of species regularly do so, and follow bathing with bouts of preening and oiling behaviour (Simmons 1964; Slessers 1970). However, in contrast to dustbathing, which has been the subject of extensive welfare-related research in domestic fowl (reviewed in Olsson & Keeling 2005), there has been little work on water bathing since some early descriptive studies.

Various hypotheses have been proposed for the benefits of water bathing. Simmons (1964) suggested that bathing serves to wet the feathers in a controlled fashion that aids the distribution of preen oil and thus enhances preening. In support of this he described observations in waders and grebes of birds wetting the bill prior to preening when no bathing has occurred. Slessers (1970) suggested that bathing serves to squeeze water through the feathers, ensuring that both skin and feather bases are rinsed. *In vitro* studies show that water has a direct impact on feather structure (Van Rhijn 1977; Elowson 1984), suggesting a different mechanism whereby bathing could affect feathers. Thus, although the precise mechanism is unclear, it seems likely that water bathing has a function in feather maintenance.

Some bird species (e.g. most members of the order galliformes, but also others including some passerine species) bathe in dust as an alternative or supplementary substrate to water. Dustbathing is similarly thought to play a role in feather maintenance, specifically in reducing ectoparasite loads and controlling the lipid content of feathers (Olsson & Keeling 2005). The latter hypothesis has been experimentally confirmed (Borchelt & Duncan 1974; Van Liere & Bokma 1987), resulting in the suggestion that there is an optimal lipid load for feathers that balances the beneficial effects of waterproofing, insulation and improved feather structural integrity against the costs of feather matting and nourishment for ectoparasites. There is some direct evidence that dustbathing in Japanese quail, *Coturnix coturnix japonica*, has a function in feather maintenance (Healy & Thomas 1973). Birds given access to dust showed an improvement in feather barb alignment immediately after dustbathing in comparison to a control group denied access to dust.

European starlings, *Sturnus vulgaris*, and the majority of passerines bathe according to the first method described by Slessers (1970, p. 92). That is, they stand in shallow water and immerse themselves through a set pattern of movements involving dipping the head and rolling the body to ensure that water is distributed widely. There is little published information regarding the bathing behaviour (frequency, seasonality, etc.) of starlings, but they are known anecdotally to be enthusiastic bathers, and recommendations for husbandry of starlings in the laboratory include provision of water baths (Hawkins et al. 2001; Asher & Bateson 2008). Our own observations of captive starlings confirm that they regularly partake in water bathing. Indeed, they commonly do so when their bathing water has been refreshed, even in the presence of a human observer. The current experiment was stimulated by our observation that birds that have just been caught and handled often bathe immediately when released into a cage or aviary containing fresh bathing water. This suggested to us that bathing, and the following preening routine, might serve a function in repairing feathers disrupted by catching and handling.

A direct test of the hypothesis that bathing facilitates feather maintenance is difficult. In order to score feather disruption it is necessary to catch and handle a bird, reversing any benefits of prior bathing. However, since plumage condition is known to affect flight performance in starlings (Swaddle et al. 1996), we hypothesise that poor feather maintenance should translate directly into reduced flight performance. We therefore tested the hypothesis that depriving starlings of the opportunity to water bathe will impair their escape flight performance, as assessed by their speed and accuracy at negotiating an aerial obstacle course. Since flight performance is likely to translate into reduced ability to escape predators or increased tendency to hit obstacles, the fitness consequences of possible effects of bathing on either speed or accuracy of flight are clear (Cuthill & Guilford 1990; Lima 1993).

METHODS

Subjects

The subjects were 32 (16 male and 16 female) adult European starlings caught from the wild under licence from Natural England. Prior to the experiment, birds were group-housed in two indoor aviaries (2.4 x 2.15 x 2.3 m) with wood chippings covering the floor, dead trees for perching and cover, and shallow trays of water for bathing. The light:dark cycle was 14:10 h and the temperature was 16-18°C. Throughout the experiment birds were fed a diet of Purina kitten food ad libitum, supplemented with fruit and mealworms (*Tenebrio* larvae). Our study was approved by the Named Animal Care Welfare Officer at the Instiute of Neuroscience, Newcastle University. Birds were inspected on a daily basis by technical staff and, following completion of our study, received a full health inspection by a veterinarian prior to their release to the wild at the site where they were originally captured.

Morphological Measures

Prior to their allocation to the experimental aviaries (see below), birds were captured by hand and several measures were taken. Weight and wing length were measured as described by Redfern & Clark (2001). It was not possible to weigh the subjects immediately prior to assessing their flight performance because handling would have disrupted any plumage condition advantages that bathing might have conferred. We scored plumage condition by assessing each primary and tail feather as either: complete, abraded, broken, growing or missing (based on Redfern & Clark 2001).

We then allocated subjects to one of three groups on the basis of how many broken and missing feathers were present: group 1: one or no feathers broken, growing or missing; group 2: two to four feathers broken, growing or missing; group 3: more than four feathers broken, growing or missing. Since plumage condition is known to affect flight performance (Swaddle et al. 1996), equal numbers of birds from each feather condition group were allocated to the four experimental groups (see below).

All birds' bills were lightly trimmed with nail clippers at this time, since bill morphology affects preening (Clayton et al. 2005). Bill trimming is a recommended standard husbandry technique in starlings, required to prevent overgrowth of one mandible by the other (Hawkins et al. 2001). For our experiment they were trimmed just enough to ensure that the mandibles were of equal length.

Bathing Manipulation

We used a 2 x 2 factorial design in which we manipulated both long- and short-term access to bathing water and assessed the effects of this manipulation on flight performance. All birds were allocated to one of two long-term groups: either an aviary with a water bath (500 x 400 x 180 mm deep) filled to a depth of 25 mm (N = 17), or an aviary with no water bath (N = 15). Birds spent a minimum of 3 days in these aviaries. The day before flight performance testing, birds were recaught and transferred to individual cages (750 x 450 x 440 mm high) located in a separate room. Birds from each long-term access group were allocated to two short-term groups: birds with short-term access to bathing water received a water bath (360 x 255 x 60 mm deep) filled to a depth of 25 mm (N = 16), whereas birds with no short-term access received an empty tray of the same dimensions (N = 16). Thus each bird fell into one of four possible treatment groups defined by the combination of long- and short-term access to bathing water it received. Although each of the four groups contained an equal number of females (N = 4 for all), one male was incorrectly allocated causing unequal numbers of males in long-term access groups (no access to water: N = 3 males; access to water only in the long-term: N = 5 males; access to water only in the short-term: N = 4 males; access to water at all times: N = 4 males).

At 0730 hours on the day of flight performance testing, the birds with baths had their baths cleaned and refilled with fresh water to encourage bathing in the 3 h immediately prior to testing. The birds without baths had their empty trays cleaned and returned to match disturbance levels. All 16 birds in the short-term access group bathed in the 3 h immediately prior to flight performance testing, but were no longer obviously wet or preening by the time testing began at approximately 1030 hours. Immediately prior to testing, each bird was induced to walk into a release cage using differential lighting conditions, and was then transported to the nearby test room. Thus, birds were not handled between the short-term bathing manipulation and flight performance testing. Birds were tested in a random order.

Testing Flight Performance

We assessed flight performance by releasing birds through an obstacle course of hanging weighted strings, and recording the number of strings hit and the speed of flight (Witter et al. 1994; Balmford et al. 2000; Swaddle & Lockwood 2003). The test room (Fig. 1) consisted of an acceleration area clear of obstacles followed by the strings. The latter comprised 38 weighted strings hanging from the ceiling, arranged in seven offset rows. The distance between strings within each row (275 mm) was approximately three-quarters of the wing-span of an adult starling. The exit from the course opened onto a well-lit escape room (5.2 x 2.3 x 2.35 m high) containing a dead tree on which birds could perch. The test room was lit only by light from the escape room to encourage the birds to fly towards the escape room on release.

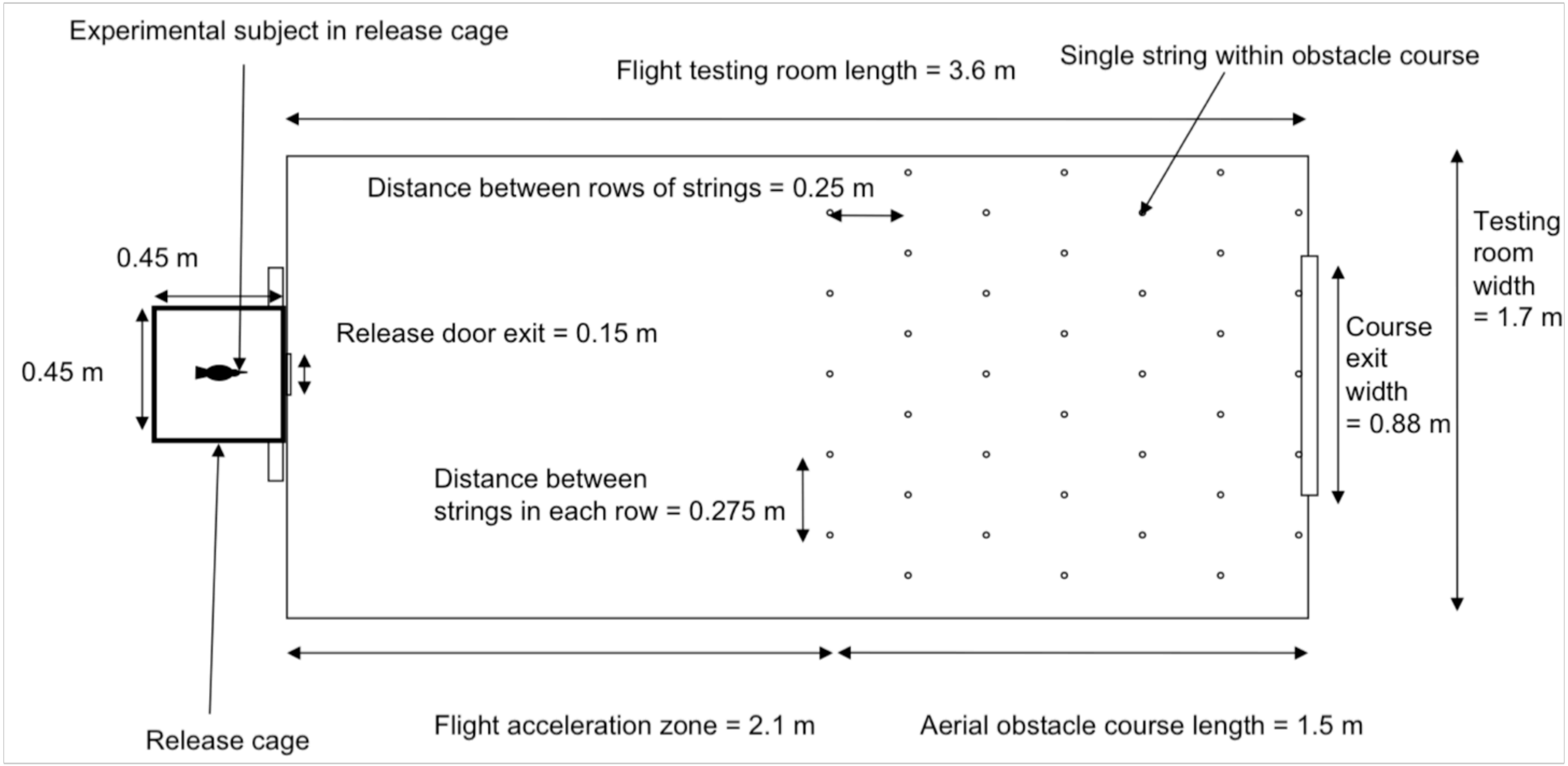

Figure 1. A plan of the test room (approximately to scale).

A release took place as soon as the bird had settled in a location facing the door of the release cage. We opened the door using a string concurrent with a standardised loud noise (a digitised recording of a bang) played immediately behind the cage from speakers at a constant volume and distance to the bird in the cage. The bird's flight was recorded on a video camera, mounted behind the release cage, running at 30 frames/s, allowing for later frame-by-frame analysis. Another camera mounted vertically above the exit from the test room simultaneously monitored the exit from the release cage (using a mirror) and the exit from the test room.

Two measures of flight performance were extracted from the data. We measured flight accuracy by recording the number of strings each bird hit as it negotiated the course. Flight time was calculated as the difference between the time of the frame when the bird passed through the door of the release cage and the time of the frame when its bill breached the exit to the escape room. Flight time was divided by the length of the test room (3.6 m) to give flight speed (m/s). All video scoring was conducted blind to the bathing treatment group of the bird.

Statistical Analysis

We used a MANCOVA to examine the effects of bathing treatment group (short term, long term and their interaction) on our two dependent measures of flight performance (number of strings hit and speed). To refine our selection of covariates, we excluded those that were highly correlated with any that had already been selected for inclusion in the model. Since body weight (g) was significantly correlated with wing length (mm) ($r_{31} = 0.535$, $P = 0.002$) it was the only size-related covariate included. We had six measures of feather damage: wing or tail feathers missing, broken or abraded. To minimise this number, we grouped any covariates that we had *a priori* reason to presume would have a similar influence. As previous studies have shown that the absence of feathers (as occurs in moult) can have implications for flight ability (Hedenström 2003), we grouped together the feathers missing and feathers broken variables. However, we chose to group only those measures belonging to the same feather group (wing or tail) since correlations between different measures from the same feather group (wing or tail) were higher than for the same measures from different feather groups. This resulted in four feather measures: wing feathers broken or missing, tail feathers broken or missing, wing feathers abraded and tail feathers abraded. Of these, the number of tail feathers broken or missing was marginally nonsignificantly correlated with weight ($\tau = 0.263$, $P = 0.076$; all other feather variables: $P > 0.48$); hence only the remaining three feather variables were included with weight as covariates. The interactions between each covariate and separate experimental factor were also initially included in the model. In line with accepted practice we excluded covariates (and their accompanying interactions) in a stepwise manner, removing the least significant term from the model in each step. The covariates were only removed on condition that the interactions with the experimental treatments were also nonsignificant (Engqvist 2005). The number of strings hit was square-root transformed prior to analysis. All assumptions of the performed tests were checked and held true. Estimates of effect size are given in the form of partial Eta squared (η_p^2) which represents the proportion of the total variance (effect + error) that is attributable to the effect. The weight for one of the subjects was inadvertently not recorded and therefore any analyses conducted where weight was included as a covariate excluded the data from this subject. Statistical analysis was conducted using SPSS version 16 (SPSS Inc., Chicago, IL, U.S.A.).

RESULTS

Our dependent variables were moderately negatively correlated ($r_{32} = -0.346$, $P = 0.052$), hence our decision to undertake a multivariate analysis of variance was justified. After we excluded all nonsignificant covariates and interactions, the resulting model included weight as the sole covariate because of the significance of the weight*short-term bathing manipulation interaction (short-term access to bathing water: $V = 0.26$, $F_{2,24} = 4.189$, $P = 0.028$, $\eta_p^2 = 0.26$; long-term access to bathing water: $V = 0.01$, $F_{2,24} = 0.128$, $P = 0.881$, $\eta_p^2 = 0.01$; interaction between short-term and long-term access to bathing water: $V = 0.07$, $F_{2,24} = 0.927$, $P = 0.410$, $\eta_p^2 = 0.07$; weight: $V = 0.12$, $F_{2,24} = 1.633$, $P = 0.216$, $\eta_p^2 = 0.12$; interaction between weight and short-term bathing manipulation: $V = 0.24$, $F_{2,24} = 3.730$, $P = 0.039$, $\eta_p^2 = 0.24$; all test statistics for the omnibus test produced identical outputs, hence only that for Pillai's trace is given here).

For two reasons we decided to refine our analysis such that the covariate interaction could be negated. First, examination of the regression slopes revealed that the interaction occurred primarily because of the differential effect of weight on the speed of the subjects in each experimental group. Speed increased with weight for birds that had bathed in the short-term, but speed decreased with weight for birds that had not bathed. This interaction was unexpected and was probably an artefact given the lack of a biologically realistic post hoc explanation for the interaction and the multiple covariate interaction terms included in the full model. Second, we were primarily interested in the effect of treatment manipulations in this study. Hence, we used the Wilcox (Johnson-Neyman) procedure to control for the heterogeneity in regression slopes (Wilcox 1987), a test that establishes the limits of the covariate for which the treatment groups differ (Quinn & Keough 2002). The procedure revealed that between weights of 68.3 and 77.4 g there was no significant difference in the speed of subjects between the two groups. We excluded any subjects from the analysis that fell outside of this range (leaving a sample size of N=20), then repeated the MANCOVA as per above. Both weight and the weight*short term bathing manipulation interaction had nonsignificant effects in this new model and hence were excluded to leave a minimal model that included only the treatment factors. It showed that short-term access to bathing water was still the only manipulation with a significant effect on flight speed and the number of strings hit (short-term access to bathing water: $V = 0.41$, $F_{2,15} = 5.170$, $P = 0.020$ $\eta_p^2 = 0.41$; long-term access to bathing water: $V = 0.25$, $F_{2,15} = 2.449$, $P = 0.120$, $\eta_p^2 = 0.25$; interaction between short-term and long-term access to bathing water: $V = 0.24$, $F_{2,15} = 2.374$, $P = 0.127$, $\eta_p^2 = 0.24$).

Having demonstrated robustly that there was an effect of the short-term bathing water manipulation, we subsequently included all subjects and conducted follow-up ANOVAs on each dependent variable. These showed that there was no significant effect of the bathing manipulations on either flight speed (short-term access to bathing water: $F_{1,28} = 2.13$, $P = 0.155$, $\eta_p^2 = 0.07$; long-term access to bathing water: $F_{1,28} = 0.32$, $P = 0.575$, $\eta_p^2 = 0.01$; interaction between short-term and long-term access to bathing water: $F_{1,28} = 0.27$, $P = 0.606$, $\eta_p^2 = 0.01$) or number of strings hit (short-term access to bathing water: $F_{1,28} = 1.98$, $P = 0.171$, $\eta_p^2 = 0.07$; long-term access to bathing water: $F_{1,28} = 0.59$,

$P = 0.449$, $\eta_p^2 = 0.02$; interaction between short-term and long-term access to bathing water: $F_{1,28} = 1.31$, $P = 0.262$, $\eta_p^2 = 0.05$) when considered individually (see Figs 2 and 3: data from all subjects are plotted). This suggests that the effect of bathing depended on the interaction of our two dependent variables.

To explore this possibility we undertook a discriminant function analysis to establish how speed or the number of strings hit contributed to the ability to distinguish subjects in the two short-term bathing experimental groups. The analysis revealed a single discriminant function with a canonical $R^2 = 0.19$. This function significantly differentiated between birds that had short-term access to bathing water or not ($\Lambda = 0.81$, $\chi^2_2 = 6.12$, $P = 0.047$). The correlation between flight performance measures and the discriminant function revealed that both measures loaded highly and positively on to this function (speed: $r = 0.947$; number of strings hit: $r = 0.936$).

DISCUSSION

Effects of Short and Long-term Access to Bathing Water

Our results show that bathing in water in the 3 h prior to a flight test had a significant impact on flight performance in starlings that had previously had their plumage disrupted by catching and handling. Birds that had bathed in the short term tended to hit fewer strings and fly more slowly through the obstacle course. Although this trend was not statistically significant when each measure was examined individually, our results suggest that the effect of short-term bathing is manifested in the trade-off between the speed of escape and the need to avoid collisions. Indeed, the discriminant function analysis shows that both speed and the number of collisions load highly on to the

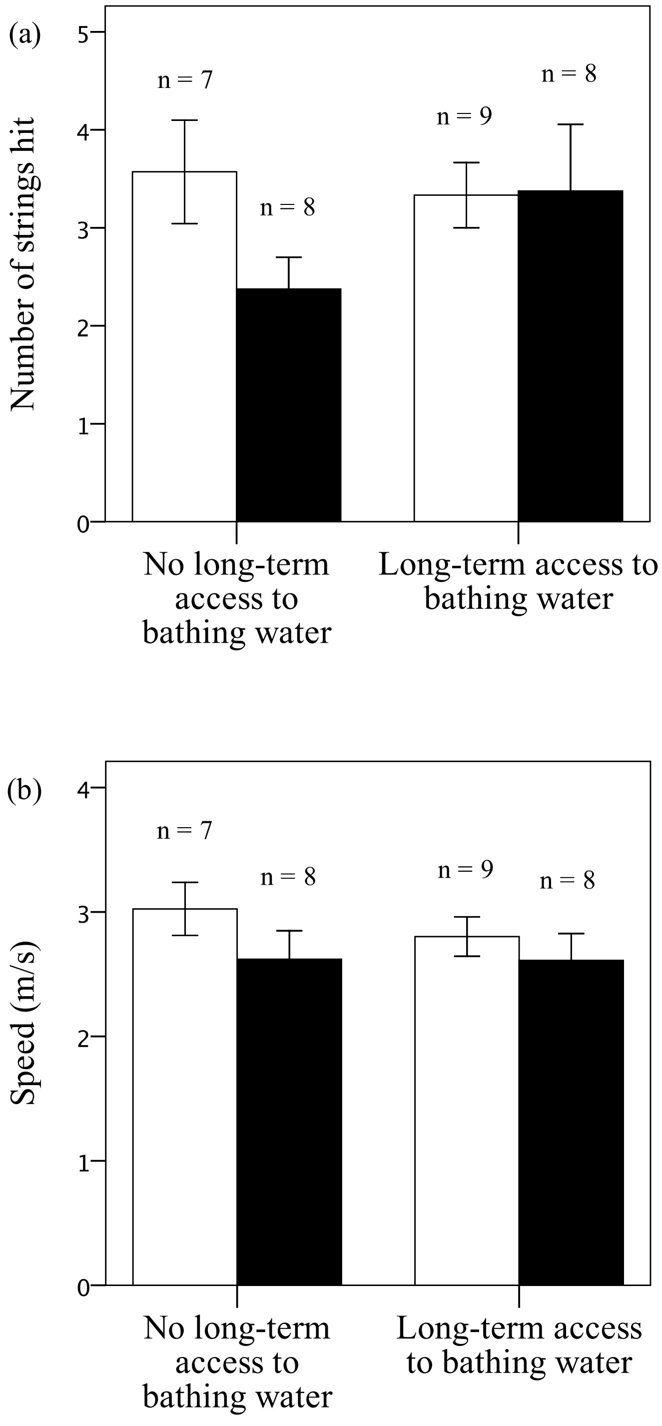

Figure 2. (a) Mean number of strings the subjects hit during flight and **(b)** mean speed subjects through the obstacle course when they had short-term and long-term access to water baths. White bars represent subjects with no access to bathing water in the short-term, black bars represent subjects with access to bathing water in the short term. Error bars represent 1 SE.

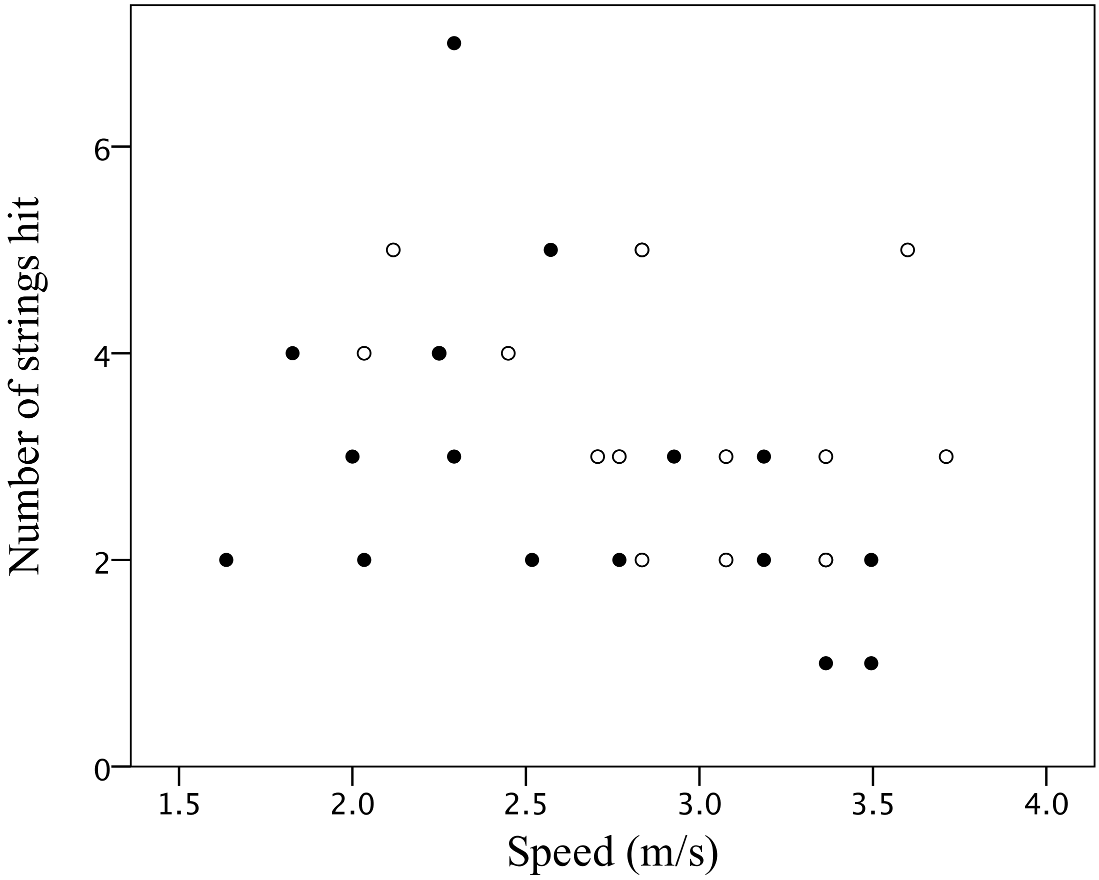

Figure 3. The relationship between speed through the aerial obstacle course and the number of strings hit. Filled circles represent the data from birds that had short-term access to bathing water. Open circles represent the data from birds that had no short-term access to bathing water.

discriminant function that enables differentiation of the two short-term bathing experimental groups. Additionally, this discriminant function had a canonical R^2 of 0.19, suggesting that the short-term bathing manipulation caused at least a medium effect size (Cohen 1992).

Relationship between Speed and Accuracy

Our results show that there was a (marginally nonsignificant) negative correlation between flight speed and number of strings hit (i.e. there was a positive relationship between speed and accuracy: see Fig. 3). However, the experimental manipulation (providing bathing water immediately prior to the flight trials) decreased both flight speed and the number of strings hit in equal measure (as indicated by the discriminant function analysis). It therefore increased accuracy but seemingly at the expense of speed. Below we discuss the implications of this finding within the context of other experimental results.

In agreement with our findings, previous comparable experiments have generally found that subjects that fly faster through an obstacle course have better accuracy in avoiding strings (but see Evans et al. 1994 for a partially contradictory finding). Swaddle & Witter (1998) found that there was no difference in flight speed in starlings with varying wing asymmetry, but that more symmetrical birds hit fewer strings and tended to be faster. Witter et al. (1994) found that manipulations of mass had no significant effect on the time taken to complete an obstacle course, but that weighted birds hit more obstacles. When a natural manipulation of mass was used (food deprivation) there was a trend for lighter birds to be faster and hit fewer strings. Similarly, an experiment with house martins, *Delichon urbica*, found that birds with distal parts of the outer tail feathers trimmed flew both faster and more accurately through an obstacle course (Matyjasiak et al. 2004). Finally, Balmford et al. (2000) showed that artificially shortening the tail length in golden-headed cisticolas, *Cisticola exilis*. resulted in decreased speed and more strings hit, while increasing the tail length resulted in increased speed and accuracy.

We propose that *within* individuals there is a trade-off between flight speed and flight accuracy. However, this trade-off is not apparent *between* individuals because higher intrinsic flight performance ability is reflected in both higher speeds and improved accuracy (in much the same way that people with larger houses also tend to own more expensive cars). This is represented conceptually in Fig. 4a, which shows a speed-accuracy trade-off within each individual (grey lines), but an overall positive correlation of speed and accuracy between individuals (black line). The parallel light grey lines in Fig. 4b demonstrate the potential effect of our experimental manipulation, namely an average decrease in speed and increase in accuracy. Figure 4b also illustrates the two possibilities for how the manipulation effected this change: either by altering the perceived escape flight payoffs for the birds causing them to consider flight speed of less importance than the reduction in collision risk (parallel dashed arrow in Fig. 4b); or by causing some mechanical change in flight performance, altering the optimality trade-off that each individual is able to make (oblique dashed arrow in Fig. 4b). These are not mutually exclusive hypotheses; indeed it is hard to conceive of how a change in perceived payoffs could occur without a proximate mechanical means (i.e. a change in flight performance).

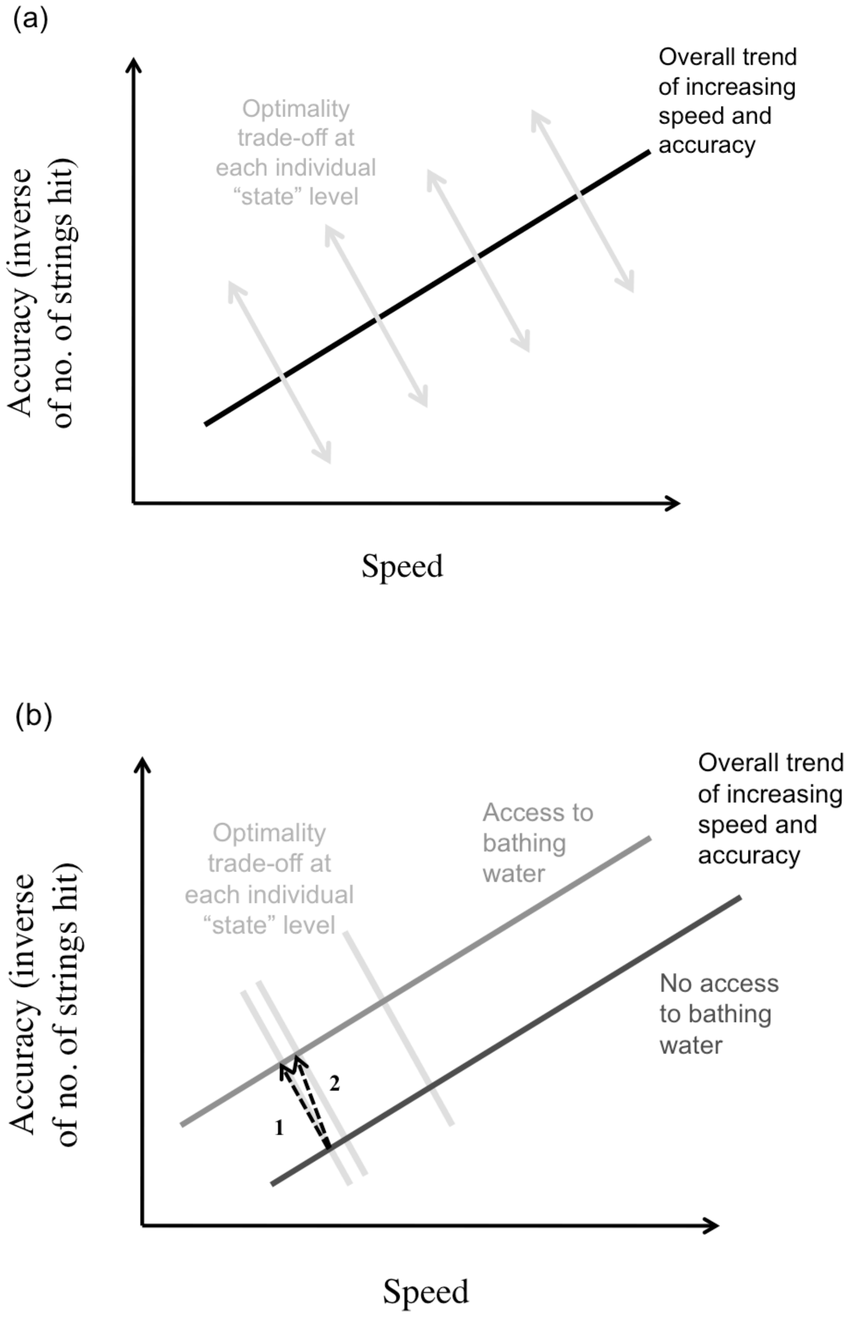

Figure 4. (a) A conceptual representation of the relationship between speed and accuracy. **(b)** A conceptual representation of the experimental manipulation effect. The dark grey line represents subjects that had no access to bathing water, the medium grey line represents subjects that did have access. The dashed black lines represent the proposed experimental effect: the parallel line (labelled 1) represents a change in the optimum of the same speed-accuracy trade-off; the oblique line (labelled 2) represents a change in mechanical flight performance causing a change in the achievable trade-off.

A number of proximate functions for bathing have been proposed that might alter flight performance: realignment of disrupted feather barbules (Healy & Thomas 1973); aiding the distribution of preen oil (Simmons 1964); enhancing feather flexibility/other mechanical effects (Van Rhijn 1977); cleansing and removal of dirt (Slessers 1970; Van Rhijn 1977); and thermoregulation (Thomas & Robin 1977; Oswald et al. 2008). The current data set unfortunately provides no means of distinguishing between these competing hypotheses. On the basis of our anecdotal evidence on the increased eagerness to bathe in birds that had been handled, we favour the explanation of realignment of feather barbules. However, we must leave the question of mechanism for future investigation.

Welfare Considerations in Captive Passerines

As a possible explanation for our results we suggest that the birds that had bathed in the short term considered the speed of escape less salient than the need to avoid collisions. This could be explicable if bathing had reduced perceived risk through a mechanical improvement in flight performance. Flight manoeuvrability is considered to be an important factor in birds' ability to escape from predators (Lima 1993; Witter et al. 1994), and reduced ability to deal with predation is reflected in an increased sensitivity to predation cues and increased aversion to risk (Stankowich & Blumstein 2005). Since anxiety is the emotional process that deals directly with awareness and interpretation of threatening stimuli (Lang et al. 2000), an increase in perceived risk of threats is likely to increase anxiety levels (Loewenstein et al. 2001). In support of our argument, we have evidence that starlings given access to bathing water subsequently show reduced sensitivity to cues of predation risk (conspecific alarm calls) (Brilot & Bateson, 2012). Additionally, captive starlings deprived of environmental enrichments, including water baths, display evidence of a more negative affective state (Bateson & Matheson 2007; Matheson et al. 2008). Similarly, reduced dustbathing results in increased fear and stress levels in junglefowl, *Gallus gallus spadiceus*, (Vestergaard et al. 1997) and domestic chickens, *Gallus gallus domesticus*, (Campo and Muñoz 2001). Selective breeding for low and high dustbathing lines in Japanese quail have also shown an inverse correlation between dustbathing and susceptibility to fear (Gerken et al. 1988). We suggest that anxiety caused by lack of water bathing or dustbathing might act as a mechanism for increasing risk aversion to avoid potential threats that could not be dealt with in an optimal fashion because of poor plumage condition. However, we accept that our data provide only circumstantial evidence to support our discussion of the relationship between bathing and anxiety.

In conclusion, we have shown that bathing alters the trade-off between escape flight speed and accuracy in starlings, providing the first experimental demonstration of a potential adaptive value of water bathing in birds. However, the proximate mechanism for the effect of bathing (mechanical or perceptual) is unresolved. We hypothesise that depriving birds of opportunities to bathe could result in increased anxiety because of a compromised ability to escape from predators.

Acknowledgments

We thank Chris Redfern, Tom Smulders and Michelle Waddle for technical help; Carel ten Cate for useful discussions; Valentin Amrhein, Steve Oswald and several anonymous referees for constructive comments on the manuscript. This work was supported by a grant awarded to M.B. from the Biotechnology and Biological Sciences Research Council (U.K.) [BB/E012000/1].

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