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ORIGINAL ARTICLE

Interaction between parent body condition and sex affects offspring desertion in response to acute stress

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Abstract

In species where the offspring are naturally deserted by one parent, the experimental stressing of breeding individuals can provide valuable information on the mechanisms underlying desertions and thus the evolution of parental roles. During a study conducted in southern Poland in 2016 and 2017, we investigated factors influencing desertion during the chick-rearing period by male and female Whiskered Terns *Chlidonias hybrida* (a species in which female desertion occurs) subjected to acute stress. We predicted that stressed females should desert their broods at a higher rate than males because of their smaller contribution to chick feeding and the probable lower cost of female desertion. For the control nests, we released birds immediately after trapping, whereas in the treatment group we temporarily removed birds from their nests, releasing them 9 or 24 h after being trapped. Birds deserted significantly more often in the treatment (28%) than in the control (7%) nests. The response to stress depended strongly on the sex-body condition interaction: in males, the probability of return to the nest after release was high and unrelated to condition, while in females the probability of return increased with body condition in both the treatment and the control groups. Breeding success in both categories of nests was not related to desertion or any of the other factors studied. This study suggests that in species where females naturally tend to desert, desertion by females subjected to disturbance may be associated with the level of their body reserves, whereas males desert at a low rate, irrespective of their body condition. More importantly, body condition appears to be an important factor that influences natural desertion.

Keywords Parental care · Removal experiment · Parental role · Disturbance · Whiskered Tern · Charadriiformes

Zusammenfassung

Interaktion von Körperkondition und Geschlecht der Eltern beeinflusst das Verlassen des Nachwuchses als Reaktion auf akuten Stress.

Bei Arten, bei denen der Nachwuchs natürlicherweise von einem Elternteil verlassen wird, kann eine experimentell verursachte Belastung von brütenden Individuen wertvolle Informationen über die Mechanismen liefern, die dem Verlassen zugrunde liegen, und somit über die Evolution der elterlichen Rollen. Während einer in Südpolen in den Jahren 2016 und 2017 durchgeführten Studie untersuchten wir die Faktoren, die das Verlassen in der Kükenphase bei männlichen und weiblichen Weißbart-Seeschwalben *Chlidonias hybrida* (eine Art, bei der ein Verlassen durch die Weibchen auftritt) beeinflussten, wenn diese akutem Stress ausgesetzt waren. Nach unserer Vorhersage sollten gestresste Weibchen ihre Brut eher verlassen als Männchen, da die Weibchen weniger zur Kükenfütterung beitragen und daher vermutlich geringere Kosten beim Verlassen der Brut durch das Weibchen entstehen. Bei den Kontrollnestern wurden die Altvögel direkt nach dem Einfangen wieder freigelassen, wohingegen in der Versuchsgruppe die Vögel für eine bestimmte Zeit von deren Nestern entfernt und erst später wieder freigelassen wurden. Versuchsnester wurden signifikant häufiger verlassen (28%) als Kontrollnester (7%). Die

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Extended author information available on the last page of the article

Stressreaktion hing stark von der Interaktion zwischen Geschlecht und Körperkondition ab: Männchen kehrten nach der Freilassung unabhängig von ihrer Verfassung mit hoher Wahrscheinlichkeit zum Nest zurück, während bei Weibchen die Rückkehrwahrscheinlichkeit in der Versuchs- und Kontrollgruppe mit der Körperkondition anstieg. Der Bruterfolg in beiden Nestkategorien hing weder vom Auftreten des Verlassens noch von irgendwelchen anderen untersuchten Faktoren ab. Diese Studie lässt vermuten, dass bei Arten, bei denen die Weibchen natürlicherweise dazu neigen, ihren Nachwuchs zu verlassen, das Verlassen durch Weibchen, die einer Störung ausgesetzt waren, möglicherweise mit der Menge an Körperreserven zusammenhängt. Dahingegen verlassen Männchen ungeachtet ihrer Körperkondition ihre Brut nur selten. Vor allem scheint die Körperkondition ein maßgeblicher Faktor zu sein, der das natürliche Verlassen beeinflusst.

Introduction

According to life history theory, animals are faced with trade-offs in the allocation of limited energy reserves to different functions (Williams 1966; Stearns 1992). During the breeding season, the allocation of resources is a trade-off between survival, reproduction and the amount of energy going into the current and future production of offspring (Clutton-Brock 1991). If, for example, fitness costs related to caring for offspring of a current breeding attempt outweigh the benefits, the parents may reduce parental care, including its complete termination, and as a consequence desert their offspring (Székely et al. 1996; Lessells 2012).

Offspring desertion (hereafter 'natural desertion') is a typical reproductive strategy resulting from a conflict between mates over their level of investment in the offspring (Székely et al. 1996; Parker et al. 2002; Lessells 2012). The conflict occurs because each parent has limited resources but aims at maximizing its own future reproductive potential by forcing its mate to invest more in the current reproductive attempt. Natural desertion allows an individual to increase its own reproductive success by leaving its mate to care for the offspring (Székely et al. 1996; Parker et al. 2002; Lessells 2012). It has been shown that natural desertion by one of a pair of mates does not usually have a negative effect on breeding success, and that the mate that continues parental care compensates for the missing deserter. On the other hand, the deserter can benefit, for example, by re-nesting and increasing his/her own reproductive success (Beissinger 1987; Fujioka 1989; Székely and Williams 1995; Roulin 2002; Bèziers and Roulin 2016). Uniparental offspring desertion in species with biparental care occurs in many bird species, particularly in the Charadriiformes, but has also been recorded in the Passeriformes (Székely et al. 1996; Griggio and Pilastro 2007). Although offspring desertion by females is generally more common in the former (Székely et al. 1996), both the males and females of some species desert, e.g. in the Kentish Plover *Charadrius alexandrinus* (Amat et al. 1999) and Red-necked Grebe *Podiceps grisegena* (Kloskowski 2003). Desertion by the male only during chick-rearing is scarce, but it has been recorded in, for example, Magnificent Frigatebirds *Fregata magnificens* (Osorno and Székely 2004).

Desertion by one or both parents is sometimes unintentionally caused by human disturbance (visits, observation, capture, handling), pressure from predators, severe weather or other external stressors (Kania 1992; Székely et al. 1996; Dubiec 2011). When birds desert under such circumstances, it is usually because they have been exposed to acute stress. In these situations, breeding adults face a dilemma: should they continue parental care or should they immediately abandon their young, thereby securing their own survival? Provoked desertion can sometimes lead to brood or clutch failure. In both natural and provoked permanent desertions, the decision whether to continue to care for or desert the offspring may depend on the sex of the potential deserter, body condition, brood size, offspring age or stage of incubation, re-mating opportunities, stage of the breeding season and the ability of the deserted mate to continue parental care—in other words, on the individual costs and benefits arising from desertion (Lessells 2012; McNamara and Houston 1996; McNamara et al. 2002).

In species with biparental care, factors affecting offspring desertion have mostly been studied during natural desertions, whereas little work has been done to examine the factors causing males and/or females to abandon their offspring during provoked desertion. Males and females may react differently to stress associated with provoked desertion (Wiebe 2010; Calisi et al. 2017). Females may be more sensitive to stress than males and desert because the cost of continuing uniparental brood care may be greater for them than for males, as has been shown in species with natural desertion (Székely and Williams 1995; Székely 1996; Wiebe 2005). This is particularly true if the physiological stress of egg laying and incubation has left females less able to perform brood care (Erckmann 1983). For example, in the Kentish Plover, a precocial species in which females desert more often than males under natural conditions, male-tended broods were found to survive better because males were better able to protect the brood from attacks by conspecifics and predators (Székely 1996). Furthermore, females may generally have other opportunities to reproduce (Székely et al. 1996; Amat et al. 1999; Wiebe and Kempenaers 2009) and therefore reduce their parental effort during the current breeding attempt (e.g. Wiebe and Elchuk 2003; Ledwoń and Neubauer 2017). Owing to the male-biased operational sex ratio in the Kentish Plover, females that have deserted have more opportunities for re-mating than males (Székely et al. 1999). Males may be able to achieve greater reproductive success from uniparental brood care than females, perhaps because of differences in inherent morphological or behavioural characteristics (Pierce 1997; Wiebe 2005; Ledwoń and Neubauer 2017). In the Whiskered Tern *Chlidonias hybrida*, a species in which it is usually only the females that desert, males, being larger than females, can provide the chicks with larger, more nutritious prey than females (Gwiazda and Ledwoń 2015; Gwiazda et al. 2017; Ledwon and Neubauer 2017). By fighting potential intruders, male Kentish Plovers protect their young more intensively than females do (Székely 1996). Moreover, in species in which one sex (usually female) naturally deserts, this sex should be more likely to cease parental care after acute stress, especially when this occurs close to the time of natural desertion. Accordingly, in these species, the male should be more resistant to stress than the female, and this will ensure his greater commitment later in the chick-rearing period.

One of the most important factors that can influence desertion (both natural and provoked) is the state of the organism (McNamara and Houston 1996), commonly measured as body condition. This affects such important aspects of reproductive performance as the decision to initiate breeding and whether or not to terminate parental care (e.g. Chastel et al. 1995; Bustnes et al. 2002; Bleeker et al. 2005). In some species, individuals in poor body condition, such as those with critically low body mass, are more likely to desert (e.g. Gauthier-Clerc et al. 2001; Bustnes et al. 2002; Dubiec 2011). For example, male King Penguins *Aptenodytes patagonicus*, when fasting, desert their eggs if their body mass has dropped to a critical level (Gauthier-Clerc et al. 2001). In the case of Great Tits *Parus major*, females in poor body condition that have been trapped and handled desert at a much higher rate than females in good condition (Dubiec 2011). In contrast, male and female Eurasian Penduline Tits *Remiz pendulinus* in good condition desert their clutch more often than birds in poor condition because they have sufficient body reserves to re-mate (Hõrak et al. 1999; Bleeker et al. 2005). Body condition has been shown to affect the extent of parental investment, including its termination, either as a sole factor or in combination with other factors such as offspring age or breeding season advancement (Székely et al. 1996; Webb et al. 2002; Dubiec 2011; Lessells 2012). Hence, the decision to desert is usually the result of several factors acting simultaneously. Understanding the response to stress may therefore provide important insights into the evolution of parental strategies.

One way of assessing the factors that influence nest desertion after exposure to acute stress is to perform a removal experiment. One mate is temporarily removed from the nest and subjected to acute stress by keeping it in captivity for a short time (a few hours or a day) or taken dozens of kilometres away from the nest and then released (e.g. Wiebe 2010; Bulla et al. 2017). Routine trapping and handling can also be treated as a kind of removal experiment (e.g. Dubiec 2011). Removing a bird from its nest, trapping it, handling it, keeping it in captivity or displacing it are all stressful situations. It has been suggested that birds view being trapped by humans as a predation event (Silverin 1998), hence their reproductive decisions following capture may be interpreted as an adaptive response to the perceived risk of predation (Székely et al.1996; Dubiec 2011). Following experimental stressing, a bird is faced by a dilemma: should it return to the nest or abandon the clutch or brood? By comparing the characteristics (e.g. sex, body condition) of individuals that desert and of those that return to the nest (i.e. did not desert) after removal, we can draw inferences about which factors are responsible for desertions following acute stress. Moreover, an individual whose partner has been removed is also stressed because he/she is forced to compensate for this loss by providing uniparental care, and may also abandon the nest. In many removal experiments involving the study of parental compensation after removal, only one sex was removed or the birds were kept in captivity throughout the breeding season (e.g. Table 6 in Wolf et al. 1988; Wiebe 2005; Aho et al. 2009; Pierce et al. 2010). Such an approach precludes the study of the influence of sex and other factors on the probability of desertion (no return to the nest after removal). To date, there appear to have been just two studies involving the removal of both sexes in species with biparental care [Northern Flicker *Colaptes auratus* (Wiebe 2010); Semipalmated Sandpiper *Calidris pusilla* (Bulla et al. 2017)] enabling the influence of sex to be studied along with some other factors on the probability of return to the nest. No removal experiments to assess the factors affecting the probability of desertion after acute stress have so far been performed in species with natural parental desertion. Such studies would be particularly helpful in explaining the factors causing desertion after exposure to a stressor. A removal experiment in species with natural desertion may also help us to discover important factors potentially influencing both provoked and natural desertion.

The Whiskered Tern is a semi-precocial species with almost exclusively female desertion during the chick and post-fledging periods (Ledwoń and Neubauer 2017). It is a socially monogamous species, with both mates making a large investment in parental care. The males feed the females before clutch completion, the females lay a clutch that represents about one-third of their body mass (usually three eggs), and both parents incubate the eggs and brood the chicks to an equal extent (Spina 1982; Cramp 1985; Betleja 2003; Paillisson et al. 2007; Ledwoń 2010). Females contribute significantly less than males to feeding the chicks (Ledwoń and Neubauer 2017). During the chick or post-fledging period, almost all females desert their offspring while paternal care continues (only 3% of deserters are males). Female desertions start when chicks are about 5 days old and no longer require intensive brooding. The majority of desertions occur from the end of the first week of a chick's life; 7% of females desert the nest between the 5th and 9th day of a chick's life, 52% of females desert during the whole chick-rearing period, and females that desert at other times do so during the post-fledging period. The termination of parental care by females has no effect on fledging success.

The main aim of this work was to establish the response of male and female Whiskered Terns to the stress associated with removal measured as the probability of returning to the nest after removal, and to determine which factors (body condition, hatching date, treatment) might also influence offspring desertion after acute stress. This is the first removal experiment to be carried out in a species with natural female desertion, enabling the probability of provoked desertion after acute stress in both males and females to be examined. It is very difficult, if not impossible, to trap Whiskered Terns and some other bird species in which one parent naturally deserts during the chick or post-fledging period just before natural desertion. This makes it hard to study the influence of current body condition on the decision to desert. The present experiment induced the removed birds to desert during the period when females naturally start to desert. Examination of the factors affecting desertion after stress in a species with uniparental natural desertion during the period when the birds naturally start to desert can shed more light on the factors that affect both provoked and natural desertion.

To assess the importance of factors influencing the probability of return after removal and release, we performed an experiment with treatment and control groups. The treatment group consisted of birds (one parent per nest) trapped and temporarily removed from the colony (see below). In the control group, we trapped and immediately released (after the standard ringing procedure) one parent per nest. We carried out the experiment when the chicks were 4–9 days old, at the time when females naturally begin to desert (Ledwoń and Neubauer 2017). We predicted that after exposure to a stressor (removal), the removed Whiskered Tern females should desert at a higher rate than males because (1) the costs of desertion are probably lower for females than for males because females naturally desert in this species (in contrast to males); (2) females contribute less to feeding the chicks, which predisposes them to desert; (3) the natural desertion of females does not reduce fledging success. Furthermore, birds in poorer body condition should desert at a higher rate than birds in better condition which are better disposed to continue parental care.

Materials and methods

General methods

We carried out the fieldwork in 2016 and 2017, on four carp pond complexes (Spytkowice, Bugaj, Przeręb, Stawy Monowskie) in the Upper Vistula River Valley, southern Poland [for a detailed description of the study area, see Ledwoń et al. (2013, 2014) and Gwiazda and Ledwoń (2015)]. All the nests in both the control and experimental groups had clutches that hatched between 15 June and 7 August (with a peak in early July). We erected plastic mesh fences around all the nests with eggs to prevent the chicks from escaping until they were able to fly [see Ledwoń et al. (2015) for a description of the enclosure]. Enclosures allow the study of breeding success because they prevent the chicks from scattering after the researcher has entered the colony; an enclosure also allows behavioural observations to be made. The enclosures had no adverse effect on either breeding success or bird behaviour (Ledwoń 2010; Ledwoń et al. 2015, 2016).

All the nests in the control and experimental groups were monitored to assess hatching dates and breeding success. The monitoring of all nests began during the early stages of incubation (up to about the 10th day after egg laying). The nests were scanned from the pond shore and inspected more closely during visits to the colony. We entered each colony ten to 12 times per breeding season at 2- to 5-day intervals. The hatching date could be deduced either from the presence of freshly hatched chicks, which could readily be identified as they were still wet just after emergence from the egg, or by the presence of the hatching star on the egg, which indicates that a chick has started hatching and will emerge from the egg within 24 h. Hatching dates were also deduced on the basis of chick wing length, during nest visits and from observations using spotting scopes on the pond shore.

Experiment

We trapped one parent in 100 nests between the 4th and 9th day after hatching (Whiskered Tern chicks remain in the nest for 21 days). In each colony, the trapped birds were randomly assigned to the control (41 birds) or experimental group (59 birds). We caught the birds at the nests with roof traps [for a detailed description of the trapping method, see Ledwoń et al. (2015, 2016)]. Each individual trapped was ringed, measured, weighed and uniquely marked with hair dye applied to small areas of the wing and tail feathers, making it identifiable from a distance. All the birds were ringed with both a standard metal ring and a white plastic ring with a unique black alpha-numeric code; they were handled on the pond shore. Approximately 0.5 ml of blood was taken from each individual for molecular sexing (Ledwoń 2011; Ledwoń et al. 2015). The birds were always trapped in the morning. While trapping, we scanned the nests to check whether both birds from each pair were present. If only one parent was present (i.e. the trapped one), we excluded it from the experiment.

After trapping and handling, the control group birds were released immediately after processing (within 1–2 h of being trapped). All the control birds from each colony were released from the same spot, on the pond shore about 100 m from the breeding colony. In the case of the control group, the time elapsing between the bird being taken out of the trap and released was relatively long (~ 1–2 h) because after being trapped, the birds were taken to the shore (up to 15 min) where they were measured and marked. Furthermore, as the birds were marked with hair dye, they had to be kept in a bag for about 15 min to allow the dye to bind with the feathers. After dyeing, the feathers were rinsed with water and dried, and this took another few minutes.

The birds from the experimental group were removed from the nests, kept in captivity and released afterwards. Two of the 59 birds from the experimental group were excluded from the analysis: in one of the nests, all the chicks died between the removal of one parent and the start of behavioural observations, while in the other, the female died before she could be released. The original aim of the removal experiment was to provoke the desertion of one of the mates in order to obtain nests with uniparental care so that we could evaluate the provisioning rate by widowed males and females. Thus, in 2016, 33 birds were released about 9 h after being trapped [~ 1700 hours Central European Time (CET)] at a distance of 77 km from the breeding colony. In 2017, twenty-four birds were released 24 h after being trapped (~ 08:00 h CET the next day) 7 km from the breeding colony site. Because only 33% of birds deserted after removal in 2016, we decided in the following year to keep the birds for a longer time after trapping in order to increase desertion events, but logistical problems prevented us from releasing the birds at the same distance as in 2016. This difference in treatment might seem crucial, but to our surprise, there were no differences in return probability after removal (see "Results" and Table 1). The removed parent was kept in a cardboard box (21 cm × 30 cm × 25 cm) in a shed that was sheltered from wind and rain. None of the birds removed in 2016 or the first 12 birds removed in 2017 were fed or watered; the other birds removed in 2017 were manually watered with an aqueous solution of glucose. In 2017, one female that was not watered died, despite the administration of an antibiotic and saline; her death was from natural causes, i.e. infection and diarrhoea (according to veterinary opinion).

Behavioural observations of the focal nests were carried out to determine whether the birds from both the control and treatment groups returned to the nest after trapping or removal, whether birds deserted naturally after returning, and to estimate breeding success. During observations from the pond shore, an observer scanned the control and treatment nests (from a distance of 50–150 m) using binoculars (15 × 56) and spotting scopes (×20–60) until the chicks were 21 days old [the expected day of fledging, i.e. when the chicks were able to leave the enclosure; see also Ledwoń and Neubauer (2017)]. Observations usually started on the day after trapping or the day when the removed birds were released and were continued every 2–4 days in the morning, for an average of 190 min per nest. In 15 nests of the treatment group, observations started on the second day after the birds had been released, but all the birds removed from these nests returned. Birds not observed on the first day after release, and a bird that deserted after trapping, were never seen again on the nest, despite repeated observations; thus, it can be safely assumed that these birds deserted immediately after removal or trapping. Furthermore, birds that deserted naturally were also never seen again on the nest [for more information about methods, see Ledwoń and Neubauer (2017)].

Data analysis

A total of 98 nests were analysed, 41 in the control group (25 in 2016, 16 in 2017) and 57 (33 in 2016, 24 in 2017) in the experimental group, with 23 females and 18 males as control birds and with 36 females and 21 males as removed parents. Using binomial generalized linear models we (1) estimated the probability of return after trapping and removal

Table 1 Number of males and females in control and treatment groups that returned or deserted in 2016 and 2017

	Males				Females			
	2016		2017		2016		2017	
	Return	Desertion	Return	Desertion	Return	Desertion	Return	Desertion
Control group	10 (99%)	1 (1%)	7 (100%)	0 (0%)	13 (93%)	1 (7%)	8 (89%)	1 (11%)
Treatment group	9 (75%)	3 (25%)	9 (100%)	0 (0%)	13 (62%)	8 (38%)	10 (67%)	5 (33%)

(treatment group) and trapping only (control group), and (2) assessed whether the desertion of one parent influenced fledgling success (measured as chick survival until the 21st day of life). We excluded two factors, chick age and the number of chicks at the time of removal, from both models to prevent overfitting the dataset and because the variation in these two factors was small: trapping and the experiment took place at a chick age of 4–9 days, and the number of chicks was two or three. The first analysis (an ordinary generalized linear model) assessed the probability of a bird returning after being either trapped (control group) or removed (treatment group). The response was a binary variable, with the ones encoding return and the zeroes desertion. The full set of predictors in the global model included the group effect (control or treatment), body condition (residuals of body mass regressed on head and bill lengths), the sex of a trapped bird, interaction between sex and body condition, interaction between sex and group, hatching date and year (the last term addressed the treatment differences in the experimental group between the 2 years; see above). In the second analysis, we used a generalized linear mixed model. The dependent variable describing fledgling success was expressed as a binary response at the individual chick level, which could be successful (chick fledged, coded 1) or unsuccessful (chick did not fledge, coded 0). The quantity modelled was the probability that a chick had fledged successfully. The global model included type of nest (a factor with four levels: birds from the treatment group that returned after removal, birds from the treatment group that did not return after removal, birds from the control group that returned to the nests after being trapped, birds from the control group that did not return to the nests after being trapped), sex of the trapped bird, year (a factor encoding for treatment differences in the experimental group) and two continuous covariates—body condition and hatching date. We incorporated nest identifier as a random effect in the model to address potential non-independence of chicks from the same nests. Continuous covariates were scaled prior to the analysis. There was no issue with collinearity—correlation coefficients between the covariates were < 0.5 in all cases. The global model and all the simpler, nested models, missing one or more terms, were fitted in the MuMIn library (Bartoń 2015) in R 3.4.3 (R Core Team 2017). Since the model weights were balanced (Supplementary Material Tables S1, S2), model averaging and model-averaged prediction was applied considering all models with Δ Akaike information criterion adjusted for small sample size (ΔAICc) < 2 in the AICcmodavg library (Mazerolle 2015).

Results

Nineteen (19%) of the 98 birds did not return to their nests, i.e. 16 (28%) of the 57 birds removed from the experimental group did not return to the nest, whereas only three (7%) of the 41 birds in the control group failed to return after being trapped (Fisher's exact test, $p = 0.01$; Table 1).

All three best-supported models (Δ AIC < 2), fitted to the data to explain the variation in the probability of return after the removal experiment or trapping, included the group effect (control or experimental), body condition, sex and sex-body condition interaction (Tables 2, 3). After model averaging, only body condition, type of group (control or experimental) and sex-body condition interaction were found to be significant. Birds from the control group returned to their nests more often than those in the experimental group (Fig. 1a, b). In both control and experimental groups, the probability of a female returning after removal or being trapped depended on her body condition—the better her condition, the greater the probability of her returning to the nest (Fig. 1a, b). The probability of males returning to the nest was not related either to the group effect or to body condition: all the males returned to their nests with the same, high probability. The differences in treatment in the experimental group between the 2 years were not significant: the probability of returning did not depend on year.

The proportions of chicks that did not fledge did not differ between the control and experimental groups. There were 15 (i.e. 14%, $n = 109$ chicks) and 21 chicks (i.e. 14%, $n = 150$ chicks; χ^2-test, $p = 0.95$) that failed to fledge in the control and experimental nests, respectively. Breeding success did not differ between the nests to which adults returned after

Table 2 Generalized linear models (GLMs) used to explain variation in probability of return in relation to body condition (*Cond.*), type of nest [control or treatment (*Group*)], hatching date (*Ha.date*), sex of trapped bird, sex-body condition interaction (*Sex-Cond.*) and sex-type of nest interaction (*Sex–Group*)

Cond.	Group	Ha.date	Sex	Sex-Cond.	Sex-Group	*df*	AICc	Δ AICc	*ω* AICc
+	+	+	+	+		6	88.1	0.00	0.16
+	+	+	+	+	+	7	89.6	1.53	0.08
+	+		+	+		5	89.8	1.67	0.07

Plus sign indicates effects included in the models. For the full set of models, see Supplementary Material Table S1

AIC Akaike information criterion adjusted for small sample size, *ω* weight

Table 3 Model-averaged coefficients and unconditional SEs from GLMs used to explain variation in probability of return in relation to body condition, type of nest (control or treatment), hatching date, sex of trapped bird, sex-body condition interaction and sex-group interaction; for abbreviations, see Table 2

Parameter	Estimate	SE	*z*	*p*
Intercept	2.621	0.777	3.330	*< 0.001*
Cond.	1.393	0.564	2.440	*0.015*
Group: experimental	− 1.714	0.810	2.090	*0.037*
Ha.date	− 0.500	0.398	1.243	0.214
Sex: male	0.673	1.024	0.650	0.516
Sex-Cond.	− 1.454	0.723	1.986	*0.047*
Sex-Group	0.352	0.984	0.354	0.723

removal or trapping (28 out of 209 chicks did not fledge, i.e. 13%) and the nests to which adults did not return (eight out of 50 chicks did not fledge, i.e. 16%; Fisher's exact test, $p = 0.94$). No covariates were found to affect breeding success (Tables 4, 5).

During the first and subsequent observation sessions, we found males but not females in three nests from which the male had been removed for 24 h, which meant that the females had deserted the nest during the male's absence or immediately after his return. One female that deserted after removal in 2017 was observed 6 days after trapping at a distance of 7 km from her first breeding colony. This female re-mated, as she was seen standing on a nesting platform while her new mate was bringing nesting material. Six of the 13 females in the experimental group that returned after removal naturally deserted later, during the chick-rearing period, while the males continued to provide parental care.

In 2017, one male was killed by his mate on returning to the nest after having been removed for 24 h. This male was chased away by his mate as soon as he perched near the nest, but as soon as he perched on the nest, his mate attacked him. The fight lasted for just a few minutes, with fatal consequences for the male. The male had been observed to be in good condition before being killed by his mate. The females in another two observed nests punished the males following their long absence (24 h), but after a few hours both mates resumed cooperation. Punishment behaviour was not observed after birds had been removed for just 9 h.

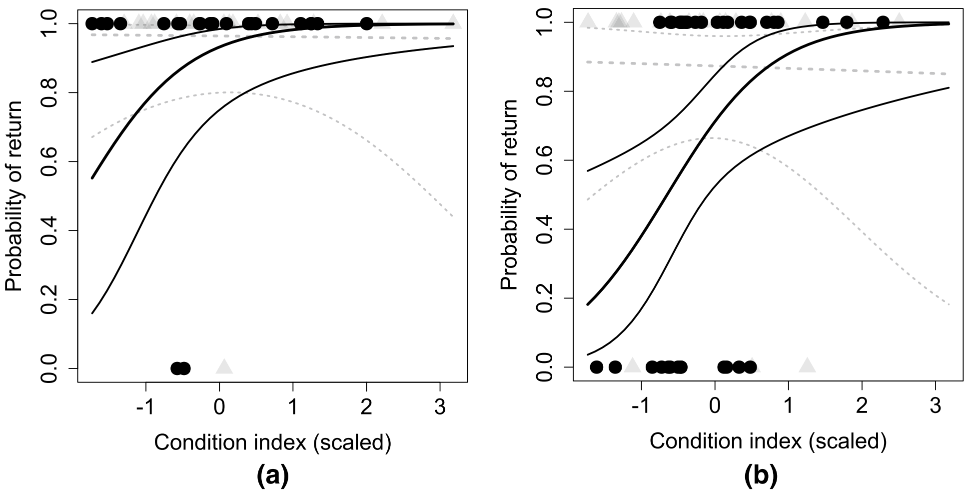

Fig. 1 Predicted relationships between probability of return of females (solid black lines and black circles) and males (dotted grey lines and grey triangles) and body condition of Whiskered Terns in control (**a**) and experimental (**b**) nests. Bold *lines* show model-averaged relationship estimated for range of condition indices observed in the data with remaining covariates fixed at their means, thin lines denote model-averaged 95% confidence intervals

Table 4 Generalized linear mixed models (GLMMs) used to explain variation in breeding success in relation to body condition of removed and trapped birds, hatching date, sex of trapped birds, year (factor including experiment type, i.e. treatment differences in the experimental group) and nest as random effect; for abbreviations, see Table 2

Fixed effects				Random effect				
Cond.	Ha.date	Sex	Year	Nest	*df*	AICc	Δ AICc	*ω* AICc
		+		+	3	211.9	0.00	0.19
Null model				+	2	212.8	0.89	0.12
+		+		+	4	213.3	1.41	0.09
		+	+	+	4	213.5	1.53	0.09
	+	+		+	4	213.7	1.79	0.08

For full set of models, see Supplementary Material Table S2

Table 5 Model-averaged coefficients and unconditional SEs from GLMMs used to explain variation in fledging success in relation to body condition of removed and trapped birds, sex of birds, year (factor including the experiment type, i.e. treatment differences in the experimental group) and hatching date; for abbreviations, see Table 2

Parameter	Estimate	SE	*z*	*p*
Intercept	2.061	0.282	7.279	*< 0.001*
Cond.	0.005	0.019	0.251	0.801
Sex: male	– 0.486	0.408	1.187	0.235
Year: 2017	– 0.039	0.170	0.228	0.819
Ha.date	0.011	0.073	0.153	0.878

Discussion

The higher desertion rate of birds in the experimental group (28%) than in the control group (7%) was most likely induced by stress caused by temporary removal. In many bird species, trapped individuals were more likely to desert when they were subjected to a more stressful procedure (e.g. Criscuolo 2001). Birds can respond to the stress associated with trapping in various ways (Kania 1992). In some species, all individuals desert after trapping, whereas in other species only a small percentage desert. The rate of desertion in Great Tits, most likely unintentionally provoked by the trapping of females during the incubation period, was very high: 41% and 26% of females deserted their first clutches during 2 study years, respectively (Dubiec 2011). Whiskered Terns appear to be relatively resistant to the stress associated with trapping, because only 3% of the birds abandoned the nest after being trapped during incubation [complete nest failure (Ledwoń et al. 2015; M. L., unpublished data)], and only 7% after being caught while brooding chicks (no total brood failure, this study, control group).

During this study, 36% of females deserted in the experimental group (between the 4th and 9th day of a chick's life; Table 1), whereas in the control group only 9% of females deserted after trapping. The latter figure is similar to that seen under natural, unmanipulated conditions, i.e. in an observational study [for detailed information about methods, see Ledwoń and Neubauer (2017)], when ca. 7% of females deserted during the same period. The percentage of nest desertions after trapping, handling and blood sampling (without temporary removal) during incubation was similar to that of the control group, i.e. 3% (Ledwoń et al. 2015; M. L., unpublished data). Thus, the birds in the control group did not desert at a significantly higher rate in comparison with unmanipulated conditions.

Females in this population naturally start to desert when the chicks are ~ 5 days old and no longer require intensive brooding. The majority (52%) of desertion events occurred during the second and third weeks of a chick's life, while the other females deserted during the post-fledging period (Ledwoń and Neubauer 2017). Our removal experiment began at the time when females naturally start to desert, and the results suggested that acute stress could accelerate natural desertion. Neither natural (Ledwoń and Neubauer 2017) nor provoked (this study) desertions reduced breeding success to a perceptible extent. In this species, males increase the provisioning rate after a female's natural desertion, thereby compensating fully or partially for the female's absence (Ledwoń and Neubauer 2017). We cannot compare our results with those of studies performed in other species showing uniparental offspring desertion, as to date no removal experiments have been carried out on them.

We predicted that removed Whiskered Tern females would be more likely to desert than males because desertion in females occurs naturally. Females make a smaller contribution to chick feeding, and males continue parental care in any case after natural female desertion; female desertions do not affect breeding success (Ledwoń and Neubauer 2017). We showed that sex alone or sex interacting with treatment (control and experimental group) was insufficient to explain the probability of a bird returning to the nest. We found that the better the body condition, the greater the probability of the female returning to the nest, whereas the probability of males returning was high, irrespective of their body condition (Fig. 1a, b). Hence, following acute stress, females were more likely to desert than males, but only those in poor body condition. This is the first time that interacting effects of sex and body condition on the probability of returning to nests after stress have been reported in birds. Two similar studies where both sexes of Northern Flickers (Wiebe 2010) and Semipalmated Sandpipers (Bulla et al. 2017) were removed showed that, despite the lack of significant differences, there was a trend for more removed females (17% and 42%, respectively) than males (5%, 0%) to abandon eggs. It was also shown that body condition of the Northern Flicker could influence the probability of return after acute stress, but the difference in body condition between birds that deserted and those that returned was not significant. In neither of these studies was the interaction between sex and body condition directly addressed. Our study indicates that during the time when natural desertion occurs, the probability that the sex that naturally deserts will return depends on body condition, whereas the sex that does not desert naturally does so at a low probability, regardless of body condition.

During the first and subsequent observation sessions after the removal experiment we found males but not females in three nests from which the male had been removed for 24 h. Females deserted the nest during the male's absence or immediately after his return. The mate whose partner has been removed is also stressed, because he/she is forced to provide uniparental care. It is probable that those females that abandoned their chicks did so because they believed the males had deserted. It is very likely that the costs for these females to resume parental care outweigh its benefits.

In our study, the half of the removed females that did not desert after being subjected to acute stress naturally did so once their chicks were older. Females in good condition did not desert: they returned to their offspring but naturally deserted later, probably choosing a more appropriate time for desertion (see below). We can therefore assume that body condition may also play a part in natural female desertion. Females in poorer body condition may naturally desert earlier than females in better condition. Body reserves may be a signal to adjust reproductive effort, and to decide to desert the nest or to return to it (e.g. Gauthier-Clerc et al. 2001; Dubiec 2011). It has been shown in penguins (Spheniscidae) that females are stimulated to forage at below their critical body mass threshold (Groscolas et al. 2000; Gauthier-Clerc et al. 2001). It is almost always the females of Whiskered Terns that naturally desert, but body condition does not differ between the sexes in this species during incubation and the first days after hatching (M. L., unpublished data). Moreover, in Little Auks (Dovekie) *Alle alle*, in which only females naturally desert, male and female body condition was not found to differ around the time of desertion (Wojczulanis-Jakubas et al. 2012). Similarly, in Kentish Plovers, where it is again mainly females that desert, the timing of natural brood desertion by females was not affected by their body condition, and body condition did not differ between males and females (Amat et al. 2000). However, female body condition in Whiskered Terns may deteriorate later, shortly before desertion. Unfortunately, it is impossible to catch females of Whiskered Tern when chicks are older and during the post-fledging period just before desertion to study body condition. The model by Barta et al. (2002) predicted that a female bird might strategically handicap herself by reducing her own body condition, as this would motivate the male to stay with her. The female, however, may exploit the male's willingness to care for the young and desert the nest. In Whiskered Terns, the probability of females deserting increased when their feeding rate decreased (Ledwoń and Neubauer 2017); this could be associated with their deteriorating body condition and consequently their progressively lower ability to feed their chicks.

Being bigger than females, males are capable of catching larger, more energy-rich prey items and in consequence provide more food to the chicks than females (Gwiazda and Ledwoń 2015; Ledwoń and Neubauer 2017); they could thus be more resistant than females to energy losses incurred as a result of feeding chicks. Differences in inherent morphological and behavioural characteristics between the sexes (Gwiazda et al. 2017) may predispose males to continue parental care after female desertion. The long period during which desertion takes place, as well as our findings that desertion after acute stress depends on body condition, indicate that the timing of natural desertion by females may depend on the body condition of both females and males. A female can consider not only her own body condition but also that of her mate. If the male is in poor body condition and the female in good condition, she may stay with him for a longer time (McNamara et al. 2002). The body condition of males and females remains to be investigated, particularly changes in the condition of both mates from the time of the egg hatching to the time of female desertion.

According to life history theory, natural selection favours behaviours that maximise lifetime reproductive success based on the trade-off between current and future reproduction (Williams 1966; Stearns 1992; Dubiec 2011). If the costs associated with continuing to care at any given moment of the reproductive cycle outweigh the benefits of such behaviour, birds are expected to abandon the current breeding attempt. In Whiskered Terns, the natural desertion of females did not lead to additional chick mortality because the males, after female natural desertion, increased the amount of food that they delivered to the chicks (Ledwoń and Neubauer 2017). The costs associated with female desertion after trapping and temporary removal therefore do not seem to be high. For females in poor body condition, the costs of resuming parental care can outweigh the benefits.

One of the proximate mechanisms underlying the propensity to desert after acute stress in Whiskered Terns in poor condition may involve the physiological effects of corticosterone. The concentration of this glucocorticosteroid is negatively related to body condition (Kitaysky et al. 1999; Adams et al. 2005) and its high level may trigger behavioural responses such as an increase in foraging activities. The corticosterone level increases rapidly in birds in response to capture and handling (e.g. Angelier et al. 2010). Therefore, if the level of this hormone is already high in a bird that is in poor body condition, the stress caused by a removal experiment may cause the level to exceed some threshold, inducing desertion behaviour. However, the probability of male Whiskered Tern returning after acute stress did not depend on body condition, which suggests that they are more resistant to the influence of corticosterone than females.

To our surprise, the differences in treatments between the 2 years, i.e. birds were released 77 vs. 7 km from the natal colony and released after 9 vs. 24 h, did not affect the probability of return after removal. It is difficult to determine what is more stressful for birds, being kept longer in captivity or long-distance removal. It seems that both procedures caused the same levels of stress in the birds.

In 2017 one male was punished and ultimately killed by his mate after returning to the nest after his temporary removal (24 h). In another two nests, females were observed to punish their mates after their long absence, although cooperation did resume after a few hours. Punishment behaviour was not observed when birds were removed for a shorter time (9 h). Females may punish their mates after a long absence because male absence may be perceived as an imminent desertion event. In shrikes (Laniidae), males punish females when they find that their mates have been copulating with a non-social male (Valera et al. 2003). However, it is very difficult to explain the killing of one's own mate. Such behaviour is not adaptive because in killing her mate the female deprives herself of her partner's assistance. Even so, the female that killed her mate succeeded in raising both of her chicks. A possible explanation for this behaviour is that the female treated the male's long absence (24 h) as desertion or death and, on his return, failed to recognise him and treated him as an alien bird. In this population, no alien birds in the vicinity of the nest are tolerated by nest owners and are always chased away. Such extreme aggression towards a mate that has been absent for a long time has not been previously reported in birds, and warrants further investigation.

The experimental manipulation in which a bird was removed from its nest and held captive could have affected it not only because of the stress that was caused. Trapping and temporary removal can decrease a bird's nutritional state and potentially weaken its bond with its mate and offspring, and can change its mate's behaviour (punishment was observed on several occasions—see above). The observed effects of the experimental manipulation, i.e. desertion, may not, therefore, only be associated with stress. It is difficult to estimate the impact of the temporary removal experiment on the birds' survival. The death of one bird while being kept in captivity was due to natural causes. One bird that deserted, 6 days after removal, reappeared on a new nesting platform at another locality. The temporary removal experiment did not appear to have an adverse effect on the birds, but this type of procedure should be implemented with caution and the effect of temporary removal on bird survival studied.

Temporarily keeping birds in captivity may negatively affect them, and even cause death (e.g. Bulla et al. 2017). To minimise the negative effects of captivity on birds, food and access to water should be provided, as appropriate for the species (see Bulla et al. 2017). Species that are unable to eat or drink on their own while in captivity should be manually watered or fed. Temporary removal of a mate can result in aggression towards them from their partner on their return; thus we recommend studying the behavioural interactions between mates after the return of one of them to the nest after a period of time in captivity (this study).

In summary, this study indicates that in a species where one sex (usually the female) naturally deserts, how the sexes respond to stress depends on the sex-body condition interaction. The probability of males returning after manipulation was high and did not depend on their body condition, whereas the probability of return in females depended strongly on body condition: the better the body condition of the female, the greater the probability that she would return to the nest. Because body condition is significantly related to female desertion after stress, we conclude that it can also influence natural desertion.

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Author contributions M. L. conceived the study; M. L., A. Ż. and A. F. collected the data; M. L. coordinated the study; A. Ż. molecularly sexed the birds; M. L. and G. N. analysed the data; M. L. and G. N. wrote the manuscript. All the authors commented on the draft version of the manuscript.

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