Incubating terns modify risk-taking according to diurnal variations in nest camouflage and ambient temperature

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Abstract

Studies of risk-taking by breeding birds have frequently addressed the effect of brood value on the decisions taken by incubating birds when predators approach their nests. However, leaving eggs unattended during predator disturbance may expose embryos to other potentially harmful factors, to which parent birds should respond when making decisions about when to leave or return to their nest. In this study we show that diurnal changes in flushing behaviour of incubating terns from nests during predator approach were affected by egg camouflage, the terns allowing a closer approach to individual nests when the eggs appeared better camouflaged. Return times to the nests were affected by ambient temperature, with the terns shortening such times at high ambient temperatures, thus diminishing the risk of egg overheating. As a whole, our results show that the decisions of the birds on when to leave or return to their nests depended on shifting payoffs, as a consequence of diurnal variations in both the thermal risks incurred by embryos and egg crypsis. Environmental costs of risk-taking, such as those considered here, should be addressed in studies of risk-taking by breeding birds. This type of study may have implications for our knowledge of cognitive processes that affect risk-taking.

Significance statement

When a predator approaches a nest, the incubating bird has to decide at which moment to leave the nest, which may be affected by environmental factors that may hamper embryo viability. We studied flushing/returning behaviour of incubating little terns *Sternula albifrons* in response to disturbance, and show that risk taking was affected by the occurrence of simultaneous environmental threats according to shifting fitness payoffs. When the eggs appeared better camouflaged, which usually occurred around

midday, the terns allowed closer approach to individual nests. The terns shortened the return to their nests with increasing ambient temperature, which took place at midday. Thus, our results show that, by adjusting their responses to shifting payoffs, the terns modulated the risks incurred by their offspring, as eggs were less time exposed to direct solar radiation in midday, when the risk of overheating was higher.

Keywords: Egg overheating • Little tern • Nest camouflage • Parental care • Payoffs • Predation risk • Predator-prey interactions • Thermal environment

Introduction

When a predator approaches a nest, the incubating bird may either flee or remain on the nest. Remaining on the nest may entail costs to the incubating adult, because if the predator approaches too close to the nest, the incubating bird might be killed (Brunton 1986; Amat and Masero 2004a). If the incubating bird flees it has to decide when to leave the nest so that it does not reveal the location of the nest to the predator. Incubating birds may also use some defensive strategies if the predator approaches close to the nest. The study of risk-taking by breeding birds, and particularly nest defence, has received much attention (Montgomerie and Weatherhead 1988; Redondo 1989; Caro 2005), because it is considered an important component of parental investment (e.g., Redondo and Carranza 1989; Amat et al. 1996; Sergio and Bogliani 2001; Cantarero et al. 2016), in which parents must weigh the probability of future reproduction against the value of the current brood (Trivers 1972). However, nest defence may also entail some types of costs that are independent of the value of the brood, and to which incubating adults vary their behaviour (Ydenberg and Dill 1986).

Birds may defend their nests actively, e.g. by using distraction displays to lure predators away, by emitting calls to silence chicks, or even by direct attack on predators (Caro 2005). However, in many species the incubating bird departs surreptitiously when a predator approaches (e.g., Amat and Masero 2004a; Troscianko et al. 2016). This may represent two serious challenges for species that nest in exposed sites with no cover, such as most Charadriiformes (shorebirds and allies). First, the incubating bird may be spotted by the predator when leaving the nest and this may facilitate nest location (Smith et al. 2012), and secondly, even if the nest is not found by the predator, the eggs may quickly cool or overheat while the nest is unattended (Grant 1982; Amat and

Masero 2007; Amat et al. 2012), thus compromising embryo survival. Because of this, the adult should leave as late and return as early as possible under adverse thermal conditions (Maclean 1967; Conway and Martin 2000a; Brown and Brown 2004; Yasué and Dearden 2006; Pereira and Amat 2010).

Many ground–nesting birds place their nests in exposed sites with no cover in which their eggs are camouflaged (Solís and de Lope 1995; Colwell et al. 2011; Gómez et al. 2016), perhaps because prevention of detection may be the primary strategy to avoid egg predation (Ruxton et al. 2004; Lee et al. 2010; Skrade and Dinsmore 2013; Troscianko et al. 2016). However, changes in illumination may induce variations in the visual perception of the eggs and nesting areas, due to either changes in illumination or the creation of shadows, which may result in variations in the degree of crypsis (Endler 1991; Endler and Thery 1996). When predators visually detect nests, deteriorating camouflage may induce an environmental cost in addition to that of maintaining the appropriate thermal environment for embryos, and because of this both the thermal and illumination factors may affect the flushing/returning behaviour of incubating adults through their effects on both egg cooling/overheating and detectability (Pereira and Amat 2010; Wilson-Aggarwal et al. 2016). Flexibility in the defensive behaviour to cope with changing conditions may increase the survival probability of eggs (Smith and Wilson 2010; Gómez-Serrano and López-López 2017).

Here, we address how variations in egg camouflage and in the thermal environment for individual nests affect flushing/returning behaviour in the ground–nesting little tern *Sternula albifrons*. We made the following predictions regarding the responses of incubating terns to disturbance: (1) incubating birds will flee at a shorter distance from an approaching predator when the nests appear better camouflaged and/or the thermal conditions are more adverse for embryos (Pereira and

Amat 2010; Wilson-Aggarwal et al. 2016); (2) birds will return sooner to their nest under more adverse thermal conditions, as beyond some temperature threshold embryos' viability may be compromised (Webb 1987; Conway and Martin 2000a, b; Yasué and Dearden 2006); and (3) returning times would not be affected by nest camouflage, because birds usually return to their nests once the predator has left the area, i.e. when there is no remaining effect of nest camouflage on nest predation risk.

Material and methods

Study site and species

Our study was conducted at Paraje Natural Marismas del Odiel (37°09'12'' N, 6°54'21'' W) during 2010, 2014 and 2015, with permission of the Consejería de Medio Ambiente (Regional Government of Andalusia). Little terns nest in loose colonies, in shallow scrapes made in the open, and which are unlined or lined with small pieces of vegetation, stones or mollusc shells (Cramp 1985). We recorded the behaviour of terns following our approach to nests (see below) from 60–200 m. Egg collection of many waterbird species was frequent during the first half of the 20th century in southern Spain (Valverde 1960), making humans an appropriate model predator of tern nests.

Field methods

We recorded the flushing/returning times at 74 nests during both the morning (06:00 – 08:30 h, GMT) and midday (10:00 – 13:45 h). The two recordings at each nest were

made on the same day, and always under clear sky conditions. Nests were chosen arbitrarily throughout the colony. It was not possible to record data blind because our study involved focal nests. One of us (first observer) approached directly the focal nest from a site (departure site), at constant pace, while another of us (second observer) observed through binoculars the incubating little tern. At the moment at which the incubating bird fled from the nest, the second observer started a stopwatch, which was stopped once the first observer arrived at the nest, and this was considered as flushing time. The first observer then photographed the nest using a Canon EOS-400 digital camera equipped with Canon EFS 18-55 mm macrozoom lens. The photographs were taken approximately 50 cm above the nest, and in jpg format. The photographic procedure took less than 3 min, and after that the first observer returned to the departure site. Once arrived to that site, the second observer started a stopwatch until the tern resumed incubation, and this was considered as return time. In a few cases, the terns resumed incubation before the first observer arrived at the departure site. In these cases the time from the moment in which the tern resumed incubation until the first observer arrived at the departure site was considered as return time and was included in the dataset as a negative value. Because of the characteristics of the nesting area, it was not possible to approach all focal nests from a similar distance.

In addition, the first observer started a stopwatch when starting to walk, and stopped it upon arrival at the nest. This was considered as approaching time, and we recorded it in about half of the nests ($n = 35$) with the aim of comparing walking pace in the morning and midday. This confirmed that approaching times to individual nests were similar during the morning ($78.3 \pm [\text{SD}] 16.03$ s) and midday (78.2 ± 15.75) (paired t -test: $t_{34} = 0.15$, $P = 0.878$).

During some days in which we recorded flushing and returning times we used eggs of Kentish plovers *Charadrius alexandrinus*, which also nest at our study site, to record egg temperatures in nests of little terns. Plover eggs are similar in size, colour and spotting pattern to those of the little tern (Cramp 1985). The plover eggs were collected from unsuccessful nests and were emptied and filled with plaster of Paris (Amat and Masero 2004b, 2007), which has a thermal conductivity similar to that of natural eggs (see Ward 1980). We placed an egg in each of 30 empty nests of little terns, i.e. nests that were without eggs and consequently not attended by adults. We used seven model eggs in which temperatures were recorded using 36-gauge copper-constantan thermocouple probes (Omega Engineering, Inc., Stamford, CT, USA) inserted into the eggs. In addition, ambient temperatures were measured at exposed sites, and 5 cm about ground level and about 1 m from nests, with 20-gauge thermocouple probes. The probes were connected to Omega OM-550 dataloggers, programmed to record temperatures every 15 sec for 10 min, since most incubating birds returned to their nests within this time period. We used the maximum egg and ambient temperatures during each of the 10 min-periods.

Analysis of images

Coloration of eggs and nest surroundings was determined from the digital photographs using MATLAB (MATLAB 2013) and the Commission International d'Eclairage (CIE) $L^*a^*b^*$ (lightness, red/green value [“redness”], yellow/blue value [“yellowness”]) colour space. We used the equation $\Delta E^* = ([\Delta L^*]^2 + [\Delta a^*]^2 + [\Delta b^*]^2)^{1/2}$ to quantify colour differences between eggs and nest surroundings (Nguyen et al. 2007; Pereira and Amat 2010; Amat et al. 2012). The lower the value of ΔE^* , the better the egg

camouflage. Lovell et al. (2013) estimated camouflage as we did, and found that laying Japanese quails *Coturnix japonica* chose those substrates in which their eggs were better camouflaged, indicating that individual quails were able to differentiate between substrates, i.e., they were able to "estimate" the degree of camouflage of their eggs against the available substrates. So, quantifying egg camouflage using this procedure seems biologically meaningful.

Once the images were read into MATLAB, two main scripts were developed. First, a graphical user interface (GUI) allowed us to define the regions where coloration differences had to be evaluated. This GUI asked how many eggs were to be marked, and requested to mark each of them using a polygonal line (MATLAB function *impoly*). Afterwards, we marked the outer border of the nest and the tool calculated what is defined as the nest area as the XOR function (logical differences) between the region inside the nest area and a region defined by the previously marked eggs which were grown by morphological dilation operation (*imdilate* in MATLAB's language) with a circular structuring element (Serra 1983) whose radius was 2.5% of the length of the egg (automatically measured from the definition of eggs' regions using MATLAB command *regionprops*). This operation simply removed a small ring of pixels around each egg from the calculation of the coloration in the nest area, thus avoiding small errors in the drawing of the egg periphery to affect the colour content of the nest area. Finally, to define the external border of the nest surroundings we separated manually about 10 mm between the external border of the nest and the beginning of what is defined as the surroundings.

Once regions had been marked, a second script was run to calculate the differences in coloration. This script tooks the folder where the images were stored as input (together with the corresponding .mat files defining the borders of each region).

For each image, the region definition file was read, and the regions were filled back and pixel coordinates generated. The script read the colour temperature when the image was shot from the EXIF data existing in each image. Information of colour temperature was then employed to obtain the $[x_D, y_D]$ chromaticity for the existing lighting conditions according to the formula defined by CIE:

$$x_D = \begin{cases} \frac{-4.6070 \times 10^9}{T^3} + \frac{2.9678 \times 10^6}{T^2} + \frac{0.09911 \times 10^3}{T} + 0.244063 & 4000 \leq T \leq 7000 \\ \frac{-2.0064 \times 10^9}{T^3} + \frac{1.9018 \times 10^6}{T^2} + \frac{0.24748 \times 10^3}{T} + 0.237040 & 7000 < T \leq 25000 \end{cases}$$

$$y_D = -3 \cdot x_D^2 + 2.870 \cdot x_D - 0.275$$

which were transformed to tristimulus values by making $Y=1$ and using the standard definition in the CIE XYZ colour space.

$$X = Y \times \frac{x_D}{y_D} \quad Z = \frac{Y}{y_D} \times (1 - x_D - y_D)$$

Finally, we employed this $[X, Y, Z]$ vector as Adapted White Point to transform the RGB to $L^*a^*b^*$, which corresponded to the lighting conditions when each image was shot (instead of using mappings associated to average illumination conditions like D65 or D50, which are standard illuminants designed to approximate natural day light conditions). Once the input image had been converted to $L^*a^*b^*$, we obtained average and standard deviation of every channel in all regions in each image.

The visual model considered here is the trichromatic, which according to Wilson-Aggarwal et al. (2016) reports similar results to those of other visual models for this type of study, and encompasses the visual systems of any likely predators of little tern eggs.

Statistical analyses

We used STATISTICA (Dell, 2015) to perform Student-paired *t*-tests to test within-nest differences in ambient temperatures, egg camouflage, and flushing times between the morning and midday. A Wilcoxon matched pairs test was used to compare return times. The effects of ambient temperature and egg camouflage on log(flushing) and log(return+50) times were analysed using linear mixed effects models (Pinheiro and Bates 2000; Zuur et al. 2009). A value of 50 was added to return times to avoid negative values. Nest identity was included as a random factor to control for non-independence between nests. Temperature and camouflage were treated as fixed effects. Year was also included as a fixed effect into the models to account for possible differences in flushing and return times among years. The residual plots were examined to check for problems with model specification. To find the significance of each fixed term in the general model we used the *F*-statistic obtained with restricted maximum likelihood (REML). Finally, model selection on fixed effects was based on Akaike Information Criterion (AIC) using models fitted by maximum likelihood (ML) estimation (Zuur et al. 2009). Linear mixed models were performed using nlme package (Pinheiro et al. 2016) in R 3.2.5 (R Core Team, 2015). We chose the model with lower AIC as the more parsimonious (Burham and Anderson 2002). Mean values are presented $\pm$ 1 SD.

Results

Ambient temperature was higher during midday (31.9 ± 4.43 °C) than during the morning (24.5 ± 2.91 °C) (paired *t*-test: $t_{73} = 16.21$, $P < 0.001$). The eggs appeared better camouflaged under the light conditions of midday ($\Delta E^* = 11.6 \pm 7.82$) than during the morning ($\Delta E^* = 20.2 \pm 9.51$) (paired *t*-test: $t_{73} = 9.70$, $P < 0.001$) (see Fig.

S1, Electronic Supplementary Material). The little terns allowed a closer approach to their nests in the midday (57.5 ± 18.27 s) than in the morning (59.9 ± 19.80 s) (paired t -test: $t_{73} = 2.69$, $P = 0.009$), and took longer to return to their nests once they were flushed in the morning (244.2 ± 314.15 s) than in midday (92.4 ± 116.26 s) (Wilcoxon matched pairs test: $Z = 5.25$, $n = 74$, $P < 0.001$). Therefore, these results indicate that, once the terns flew from their nests, the eggs remained exposed to direct solar radiation more time during the morning than during midday.

For eggs exposed to direct sunlight, there was a very significant relationship between egg and ambient temperatures ($r_{28} = 0.92$, $P < 0.001$; Fig. 1), and at ambient temperatures $>32^{\circ}\text{C}$ the eggs reached temperatures that may be lethal for embryos ($>40^{\circ}\text{C}$, Webb 1987) in only one minute when left unattended (Fig. 2).

The two dependent variables (flushing and return times) analysed using linear mixed models were not affected by the same factors. In addition to year, egg camouflage, but not ambient temperature, significantly affected the flushing behaviour (Table 1). The AIC of the model that did not contain the ambient temperature effect (-43.37) was lower than that of the general model (-31.32). The terns allowed a closer approach when their nests appeared better camouflaged (lower values of ΔE^*) ($\beta = 0.004$ [SE 0.001], $t = 3.075$, $P = 0.003$) (Fig. 3A). Return times to the nests were significantly related to year and temperature, but not to egg camouflage (Table 1). The model that related return time to year and temperature was better (AIC = 331.54) than the general model (AIC = 340.00). Return times to the nest were shorter when ambient temperature increased ($\beta = -0.0667$ [SE 0.011], $t = -6.159$, $P < 0.001$) (Fig. 3B).

Discussion

Many studies of nest defence have addressed the effect of the reproductive value of the clutch and/or expectation of future reproduction on the responses of birds when their nests are threatened (e.g., Redondo and Carranza 1989; Forbes et al. 1994; Amat et al. 1996), but fewer studies have considered the importance of abiotic factors (e.g., Brown and Brown 2004; Kleindorfer et al. 2005; Yasué and Dearden 2006). Our results show that there was interannual variation in return times, which may be related to annual differences in ambient temperature (data not shown). Flushing distances were also affected by year, likely in relation to the distances from which we approached nests. Indeed, this has been shown in other studies to affect flushing distances (Kleindorfer et al. 2005; Weston et al. 2012). After controlling for yearly effects, in our study the flushing distances and the return times to nests varied according to prevailing environmental conditions that may affect the vulnerability of eggs, through its effects on embryo viability (ambient temperature) and nest detectability (illumination), in a way that has been previously rarely examined (e.g., Pereira and Amat 2010; Wilson-Aggarwal et al. 2016).

As the terns were not marked we were unable to know which sex was incubating during each visit. In some biparental species, the sexes divide their duties during day and night (e.g., Fraga and Amat 1996; Ekanayake et al. 2015). In a study on the little tern both sexes incubated during diurnal time, though females spent about 25% more time incubating than males (Fasola and Saino 1995). Nevertheless, the patterns of sex allocation to incubation in terns seem to be very variable, as multiple studies conducted on the same species in different years or areas have produced contrasting results (see Fasola and Saino 1995). When we split the results between morning and midday, flushing times in our study were still affected by egg camouflage, and return times by

temperature (Table S1, Electronic Supplementary Material), suggesting that the sex of the incubating bird would not affect the results if one sex incubates in the morning and the other during midday.

It has been suggested that when an observer repeatedly visits a nest, nest-defence behaviour of parents may be modified by positive reinforcement and loss of fear (Knight and Temple 1989). Indeed, birds nesting in beaches frequently visited by humans allow closer approaches to nests before flushing than birds nesting in beaches less frequently disturbed by humans (e. g., Lord et al. 2001; Faillace and Smith 2016). Although we recorded flushing behaviour first in the morning, and then during midday, our results were not likely affected by a habituation effect related to the order of visits to nests. This is because our study area was daily visited by humans, even more during weekends, so that the little terns were habituated to human presence, well before we initiated our study (see St Clair et al. 2010). After controlling for visit order to nests, Wilson-Aggarwal et al. (2016) found that flushing behaviour of shorebirds was affected by the level of camouflage of their nests.

Although brood value may affect the responses of adult birds during the defence of their offspring (see Palestis 2005, for a tern species), it is unlikely to have affected our results, as for each nest the experiments on individual nests were carried out in the same day. In our case, the environmental costs experienced by incubating terns were therefore independent of the value of the brood, and such type of environmental costs should be considered in studies of risk-taking by breeding birds.

As predicted, incubating birds flushed at shorter distances when the nests appeared better camouflaged (as also found by Wilson-Aggarwal et al. 2016) independently of ambient temperature. This may be so because when a predator approaches a nest, egg temperature is likely optimal for embryogenesis since the nest is

being attended by an adult, i.e. temperature at such moment is not a factor that may negatively affect embryos. Nevertheless, only after the adult have departed from the nest the temperature may negatively affect embryos receiving direct sun radiation, especially under hot conditions. Likely because of this, return times were affected by ambient temperature (as also found by Brown and Brown 2004; Yasué and Dearden 2006), but not so by egg camouflage as the birds usually return to their nests once the predator has left the area, i.e. when there is no effect of nest camouflage on nest predation risk. Indeed, the terns returned sooner to their nest during midday than during the morning, probably because overheating is much more harmful for embryos than cooling (Webb 1987).

Taken together, our results show that incubating little terns allow a closer approach to their nests during midday before flushing because the nests may appear better camouflaged under the light conditions of such period. Thus, our results support the predictions of Ydenberg and Dill (1986), in that flushing distances decreased with increasing the cost of flight. Because return times are also shortened with increasing ambient temperature during midday, with these strategies the terns may reduce the periods in which eggs in unattended nests may be exposed to overheating (Yasué and Dearden 2006; Pereira and Amat 2010).

An implication of our study is that individual birds may “know” how the appearance of their own eggs varies depending on short term variations in illumination conditions, and adjust their flushing behaviour from nests accordingly, a possibility that requires experimental confirmation, e.g. by analysing the responses of the birds when the camouflage of their eggs is manipulated (see also Wilson-Aggarwal et al. 2016). Japanese quail females choose nesting substrates in which their eggs appear better camouflaged (Lovell et al. 2013), suggesting that there is a cognitive process in the

selection of nesting substrates. The terns apparently also “know” how the eggs cool or heat depending on ambient temperature while the nest remains unattended. Thus, the birds not only perceived the risk of predation, but also the thermal risks incurred by embryos when their nests were left unattended. The assessment of risk to several simultaneous threats must be beneficial, and may facilitate dynamic risk taking during predator disturbance according to shifting fitness payoffs (Enquist et al. 1990). It seems therefore evident that leaving a nest unattended during predator disturbance may be a complex behaviour that not only depends on biotic factors (e.g., the reproductive value of the clutch), but also on abiotic factors that may affect reproductive performance, and its study may inform on the cognitive processes that determine decision taking.

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Compliance with ethical standards

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Conflict of interest The authors declare no conflict of interest.

Ethical approval Consejería de Medio Ambiente from the Junta de Andalucía (Regional Government) gave permission to conduct the study.

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Table 1 Results of the mixed-effects models examining the effects of year, temperature, and egg camouflage on flushing and return times to nests. Nest identity was included as a random effect

Response variables	Predictors	Num DF	Den DF	<i>F</i>	<i>P</i>
Flushing time	Intercept	1	72	1119.67	<0.001
	Year	2	71	16.94	<0.001
	Temperature	1	72	0.24	0.628
	Egg camouflage	1	72	6.47	0.013
Return time	Intercept	1	72	185.98	<0.001
	Year	2	71	17.039	<0.001
	Temperature	1	72	20.76	<0.001
	Egg camouflage	1	72	1.46	0.231

Num DF: number of degrees of freedom in the model.

Den DF: number of degrees of freedom associated with the model errors.

F: *F*-statistic obtained using restricted maximum likelihood.

P: significance

LEGEND TO FIGURES

Fig. 1 Relationship between egg and ambient temperatures in unattended little tern nests exposed to direct solar radiation. Regression line: Egg temperature ($^{\circ}\text{C}$) = $-12.170 + 1.543 \times \text{Ambient temperature } (^{\circ}\text{C})$. Kentish plover eggs filled with plaster of Paris were used to record egg temperatures

Fig. 2 An example showing how quickly an egg reaches hyperthermic conditions ($>39^{\circ}\text{C}$) once it remains exposed to direct sunlight (time = 0) at an ambient temperature of 34.5°C . A Kentish plover egg filled with plaster of Paris was used to record egg temperatures

Fig. 3 Partial plots ($\pm 95\%$ CI, in grey), controlling for year effects, resulting from linear mixed models of (A) flushing time from nests in relation to egg camouflage (lower values of ΔE^* correspond to better egg camouflage), and (B) return time to nests in relation to ambient temperature for the little tern

539 Figure 1

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542 Figure 2

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Behavioral Ecology and Sociobiology

Incubating terns modify risk-taking according to diurnal variations in egg camouflage and ambient temperature

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Nest 34, 09/07/2014

Time: 08:23

Time: 12:11

Nest 1, 14/06/2010

Time: 08:49

Time: 12:23

Fig. S1 Pictures of individual little tern *Sternula albifrons* nests at different times of day

Nest 25, 12/06/2014

Time: 08:32

Time: 11:55

Fig. S1 Continued

Table S1 Results of the mixed-effects models examining the effects of year, temperature, and egg camouflage on flushing and return times to nests during the morning and midday.

Flushing - morning

Source	Nparm	DF	DFDen	F Ratio	Prob > F
Year	2	2	69	18.0860	<0.0001
Temperature	1	1	69	0.1893	0.6649
Camouflage	1	1	69	11.0110	0.0014

Flushing - midday

Source	Nparm	DF	DFDen	F Ratio	Prob > F
Year	2	2	69	16.0719	<0.0001
Temperature	1	1	69	0.3641	0.5482
Camouflage	1	1	69	3.8763	0.0530

Return-morning

Source	Nparm	DF	DFDen	F Ratio	Prob > F
Year	2	2	69	2.1911	0.1195
Temperature	1	1	69	4.1763	0.0448
Camouflage	1	1	69	2.1523	0.1469

Return-midday

Source	Nparm	DF	DFDen	F Ratio	Prob > F
Year	2	2	69	32.0312	<0.0001
Temperature	1	1	69	4.1138	0.0464
Camouflage	1	1	69	0.0356	0.8508

Nparm: number of parameters.

DF: number of degrees of freedom in the model.

DFDen: number of degrees of freedom associated with the model errors.

F Ratio: *F*-statistic obtained using restricted maximum likelihood.

Prob > F: significance.