DABBLING DUCKS INCREASE NEST DEFENSE AFTER PARTIAL CLUTCH LOSS

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Abstract. Predation is the primary source of mortality of dabbling duck nests, so a key aspect of parental investment is defending the nest from predators. The hen's presence on the nest is widely considered to be a good measure of nest defense; an incubating female camouflages the nest and may physically deter nest predators. Parental-investment theory suggests that investment should increase with the reproductive benefits expected from the current clutch of eggs. We used nest-temperature loggers to study how the rhythms of waterfowl incubation changed after the nest was partially destroyed by a predator. Contrary to the expected-benefits hypothesis, we found that hens significantly increased their investment after partial clutch loss: they took fewer recesses from incubation per day and extended their incubation by more than 200 min after a partial depredation. We suggest that when predators pose little risk to the incubating adult, those hens unable or unwilling to abandon a nest after partial clutch loss will increase parental investment to obtain at least some reproductive benefits.

Key words: incubation, Gadwall, Mallard, nest attendance, parental investment, predation, waterfowl.

Los Patos de Genero *Anas* Aumentan la Defensa del Nido luego de la Pérdida Parcial de la Nidada

Resumen. La depredación es la causa principal de mortalidad de los nidos de los patos de superficie, por lo que un aspecto crucial de la inversión parental es la defensa del nido de los depredadores. La presencia de la hembra en el nido es ampliamente considerada como una buena medida de defensa del nido; una hembra incubando camufla el nido y puede amedrentar físicamente a los depredadores. La teoría de la inversión parental sugiere que la inversión debe aumentar con los beneficios reproductivos esperados de la eclosión de la nidada de huevos. Empleamos registradores de temperatura del nido para estudiar cómo el ritmo de incubación de las aves acuáticas cambió luego de que el nido fuera parcialmente destruido por un depredador. Contrariamente a la hipótesis del beneficio esperado, encontramos que las hembras aumentaron significativamente sus inversiones luego de la pérdida parcial de la nidada: interrumpieron menos veces la incubación por día y extendieron la incubación más de 200 min luego de una depredación parcial. Sugerimos que cuando los depredadores representan un riesgo menor al adulto que incuba, aquellas hembras que no puedan o no estén dispuestas a abandonar un nido luego de su pérdida parcial aumentarán la inversión parental para obtener al menos algunos beneficios reproductivos.

INTRODUCTION

According to parental-investment theory, individuals expending resources on the current reproductive effort may face lower survival and/or a reduction in their capacity to reproduce in the future (Trivers 1972, Maynard Smith 1977). In many precocial birds, such as waterfowl, nest attendance is a major aspect of parental investment (Afton and Paulus 1992), and, as theory predicts, investment in the current clutch of eggs imposes costs on the incubating female. High levels of nest attendance limit opportunities to forage and result in poorer body condition (Afton and Paulus 1992, Conway and Martin 2000), and incubating females may risk their own safety by remaining on the nest as a predator approaches (Montgomerie and Weatherhead 1988, Gunness et al. 2001).

Nest predation is the primary source of mortality to offspring of most bird species (Ricklefs 1969), including waterfowl (Klett et al. 1988, Sargeant and Raveling 1992,

Greenwood et al. 1995), so most aspects of parental investment involve defense against predators. Birds may change their investment strategies to manage the risk of nest predation, especially by altering nest activity (Lima 2009). Greater activity at the nest increases potential cues to predators and thus increases the risk of predation (Skutch 1949). Accordingly, in response to elevated predation risk, many passerines decrease total trips to and from the nest by increasing their attendance at the nest (Martin et al. 2000a, b, Massaro et al. 2008). In environments where the risk of nest predation is high, natural selection favors both infrequent recesses from attendance to reduce the probability of a predator detecting the nest *and* short recesses to ensure healthy development and shorter incubation times (Webb 1987, Martin 2002, Reid et al. 2002, Cook et al. 2005, Wang and Beissinger 2011). High-quality individuals may be able to reduce both the frequency and duration of recesses simultaneously (Hansson et al. 2003, Tombre et al. 2012), but others may suffer reductions in

current (Nord and Nilsson 2012) and future reproductive output (Hansson et al. 2005).

Birds may also increase levels of nest defense in response to elevated predation risk (Lima 2009); however, unlike birds that actively and aggressively defend their nests, ground-nesting dabbling ducks typically avoid direct confrontations with predators. Rather, the cryptic coloration of the incubating female makes the nest more difficult to detect (Kreisinger and Albrecht 2008) and may compensate for a nest being placed in sparse vegetation (Cresswell 1997, Remeš 2005). Additionally, the presence of an incubating female may deter some nest predators or physically block their access to eggs (Thompson and Raveling 1987, Komdeur and Kats 1999, Samelius and Alisauskas 2001, Opermanis 2004). Therefore, in waterfowl, nest attendance is often equated with nest defense and is believed to be a good indicator of parental investment in nest safety. The waterfowl literature tends to focus primarily on absolute levels of nest attendance, rather than visible levels of nest activity (Skutch hypothesis) found in the passerine literature, perhaps because predators of waterfowl nests are typically mammalian and locate nests through olfaction.

In waterfowl, overall levels of nest attendance per se are difficult to measure; therefore, studies of parental defense often use the distance at which the female flushes as a human approaches the nest as a measure of risk taking and a proxy for nest defense/parental investment. Females should defend the nest more (flush at shorter distances) when the expected fitness benefits of an attempt at reproduction are high (Montgomerie and Weatherhead 1988). Indeed, nests in later stages of incubation and nests with larger clutches are associated with shorter flushing distances (Mallory and Weatherhead 1993, Forbes et al. 1994). Additionally, ambient predation risk can attenuate the expected benefits of a nest: clutches laid in areas of high predation risk are less likely to survive, and parents should invest less. Accordingly, Forbes et al. (1994) showed that hens flush at greater distances with an investigator's subsequent visits to the nest (increasing human "predation risk"), though see Mallory and Weatherhead (1993) for an exception. Females may also be able to respond to a lack of predators by increasing investment; waterfowl flush at shorter distances when nest predators are removed from a study site (Dassow et al. 2012).

While most studies have used flushing distance upon human approach as a proxy for nest defense (Mallory and Weatherhead 1993, Forbes et al. 1994, Gunness and Weatherhead 2002, Dassow et al. 2012), the reliability of this measure depends on whether the hen considers humans to be a threat to the nest. We suggest that this assumption is questionable: unlike true nest predators, human investigators revisit nests repeatedly but never depredate eggs, are not influenced by cryptic females incubating, and are never dissuaded by the presence of a female. Additionally, flushing distance may depend on factors not associated with parental investment. For example, we have noted at our study site that flushing distance can depend on the time of day, weather, nest vegetation, speed of human approach, direction of approach in relation to nest vegetation, etc.

A second category of research on parental investment in waterfowl has focused on how investment changes in response to direct risk from actual nest predators. A series of studies by Ackerman and colleagues studied the nest-abandonment decisions of hens in response to partial depredation of a clutch. At our study site, partial loss of a clutch to predators is common in waterfowl: one study showed that approximately 30% of nests experienced at least one instance of partial depredation (Ackerman and Eadie 2003). Ackerman et al. demonstrated that waterfowl use expected benefits to make abandonment decisions; larger clutches and clutches at later stages of incubation are less likely to be abandoned in response to partial depredations (Ackerman and Eadie 2003, Ackerman et al. 2003).

While Ackerman et al. (2003) studied nest abandonment in response to partial depredations, our study measured changes in parental investment in those nests *not* abandoned after partial clutch loss. Rather than using flushing distance, we used actual nest-attendance data as a measure of parental investment, which may be a better proxy for defense against the pervasive threat of actual predators. Using nest temperature loggers placed in the bottom of duck nests, we studied how incubation rhythms changed in response to a partial depredation. Following the expected-benefits hypothesis (explored by Ackerman et al. 2003), we predicted that parental investment should decrease—females should take longer and more frequent incubation breaks—after partial depredation, because of a decrease in expected benefits. Alternatively, if the Skutch hypothesis holds true, we should predict that females will take longer and less frequent breaks to reduce nest activity and thus decrease the provision of cues to predators. Finally, the thermal inertia of a clutch may be important: smaller clutches cool faster than larger clutches (Reid et al. 2000, 2002, Boulton and Cassey 2012), so a reduction in clutch size might force females to take shorter incubation breaks more frequently ("thermal-inertia hypothesis") as they trade off maintaining nest temperature and foraging.

METHODS

We conducted our study in 2009 and 2010 at Grizzly Island Wildlife Area in the Suisun Marsh of California (38° 08′ N, 121° 59′ W), in an 800-ha block of upland fields managed by the California Department of Fish and Game as habitat for nesting waterfowl. This section of uplands is divided into fields (5–30 ha each) by dirt roads, ditches, and levees. There are a variety of habitat types available to the Mallards (*Anas platyrhychos*) and Gadwall (*A. strepera*) that nest at our site, including mid-height (<1 m) grasses (*Bromus* spp., *Lolium* spp., *Hordeum* spp.), tall (>1 m) grasses (*Elytrigia* spp., *Phalaris* spp.), herbs (*Atriplex patula)*, vetch (*Vicia* spp.), pickleweed (*Salicornia virginica*), and thistle (family Asteraceae). The primary predators on Grizzly Island are Striped Skunks (*Mephitis mephitis*) and Raccoons (*Procyon lotor*), though Coyotes (*Canis latrans*) and Common Ravens (*Corvus corax*) are also present.

We searched the fields every 3 weeks from 1 April through early July, following standard protocols (Klett et al. 1986, Gloutney et al. 1993) slightly modified by McLandress et al. (1996) for this study site. To find nests, we strung a 50-m rope between two all-terrain vehicles and dragged the rope across the top of the vegetation, flushing females from the nest. Because of the tall vegetation found at our study site, to generate additional noise, we attached tin cans containing rocks every 2 m along the rope (McLandress et al. 1996). After nests were located, we marked them with a 2-m bamboo stake placed 4 m north of the nest and a shorter stake placed at vegetation height next to the nest bowl. We recorded their locations with a Garmin GPSMAP 76 GPS receiver (Garmin International Inc., Olathe, KS) and revisited them on foot every 7 days until nest hatching or failure. We determined the incubation stage of the nest by candling the eggs (Weller 1956) and calculated the date of nest initiation by subtracting the nest's age when found (number of eggs when found plus the incubation stage) from the date the nest was found. Nests that were partially depredated when found (as evidenced by eggshell fragments at the nest) were excluded from analyses. We considered a partial depredation to have occurred when one or more eggs were missing or destroyed when we checked the nest.

We placed iButton thermochrons (model DS1921G-F5#, Maxim Corporation), glued to the top of 7.6-cm wooden golf tees, in a subset of the nests we located in 2009 and 2010. The tee was pushed into the ground through the bottom of the nest so that the iButton logger rested at the surface of the nest bottom in direct contact with the eggs. The iButton did not log the exact temperature of the eggs; rather, it recorded the relative temperature of the nest as the females left on incubation breaks and then returned to re-warm the clutch. The iButtons recorded the relative temperature of the nest every 5 min for 1 week, after which point the logger's memory was filled. In most nests, we replaced the iButton every week until the nest was terminated. Early in the season, we placed an iButton in every nest we found until we ran out of loggers. After that, replacing iButtons was prioritized for nests where loggers had already been placed, so as to record complete incubation information for a single hen. Because one goal of using the temperature loggers was to detect the timing of depredation, we preferentially placed iButtons in fields where we thought predators to be particularly active.

Using the programs Rhythm (Cooper and Mills 2005) and Raven (Bioacoustics Research Program Cornell University, Ithaca, NY), we graphed the iButton data as a time series of temperatures. Rhythm is programmed by the user to search for and automatically highlight highs and lows characteristic of typical incubation breaks, though minor manual corrections are often necessary (Cooper and Mills 2005). Before leaving for an incubation recess, the hen covers the nest with down to help maintain nest temperature while she is away. Thus a typical incubation recess is characterized by a negative linear slope as the nest temperature drops at a slow, steady rate (Fig. 1) (Boulton and Cassey 2012). When the female returns to the nest, she moves the down that was covering the nest to the periphery of the nest bowl and places her breast in direct contact with the eggs. As a result, the eggs are warmed at a faster rate than they cooled, resulting in a steeper positive slope. Predation can be identified by examining the nest-attendance graphs in combination with data taken at the nest. Predation that occurs while a female is incubating is characterized by a very steep negative slope because the female is flushed from the nest before she can cover it with down (as she would before an incubation recess) (Fig. 1). Logger graphs implying a partial depredation always coincided with a partial depredation observed at the nest.

STATISTICAL ANALYSES

For each partially depredated nest, we calculated the duration of incubation shifts and recesses, both before and after the partial depredation (or the first partial depredation, if there was more than one). We ran a mixed-model analysis in the package lme4 (Bates et al. 2011) in R 2.14. We modeled the durations of incubation shifts and recesses as a function of species, nest age, Julian date, and whether or not the nest had been partially depredated ("pd-status"). For those nests where the magnitude of clutch reduction was known ($n = 21$), we also included (centered) clutch size in our model, as well as a term for interaction of clutch size with pd-status. Because ambient temperature may also affect the incubation behavior of nesting birds, we included the daily mean and minimum temperature (°C) from a nearby (~10 km) weather station. Finally, we included nest as a random effect to account for behavioral variation among individual hens.

In addition to modeling the shifts and recesses of incubating females, we also examined how the frequency of incubation recesses changed after a partial depredation. Because the typical hen only took one or two recesses per day, calculating an "average" frequency of recesses was possible only for nests with several days of data both before and after a partial depredation. For those nests with at least 3 days of complete data before and after a partial depredation ($n = 13$), we used a paired t-test to examine how the frequency of incubation recesses changed following partial clutch loss. All values reported are means ± SE unless otherwise noted.

RESULTS

We found 311 duck nests in 2009 and 915 nests in 2010 for a total of 1226 nests. Of these, 169 (14%) were partially depredated, and 75 (44%) of these were immediately abandoned by the female. From the remaining 94 nests that were partially depredated but not abandoned, we recorded more than 400 nest-days of incubation data from 28 different nests. Our sample included data from both Mallard ($n = 19$) and Gadwall ($n = 9$) nests initiated throughout the nesting season (range 3 April–4 June).

Incubation shifts lasted approximately 12 hr (715 ± 19 min), though there was substantial individual variation; for example, one female was observed on multiple occasions to incubate the nest for >36 hr without a recess. Recesses typically lasted approximately 3 hr (171 ± 5 min), and the average
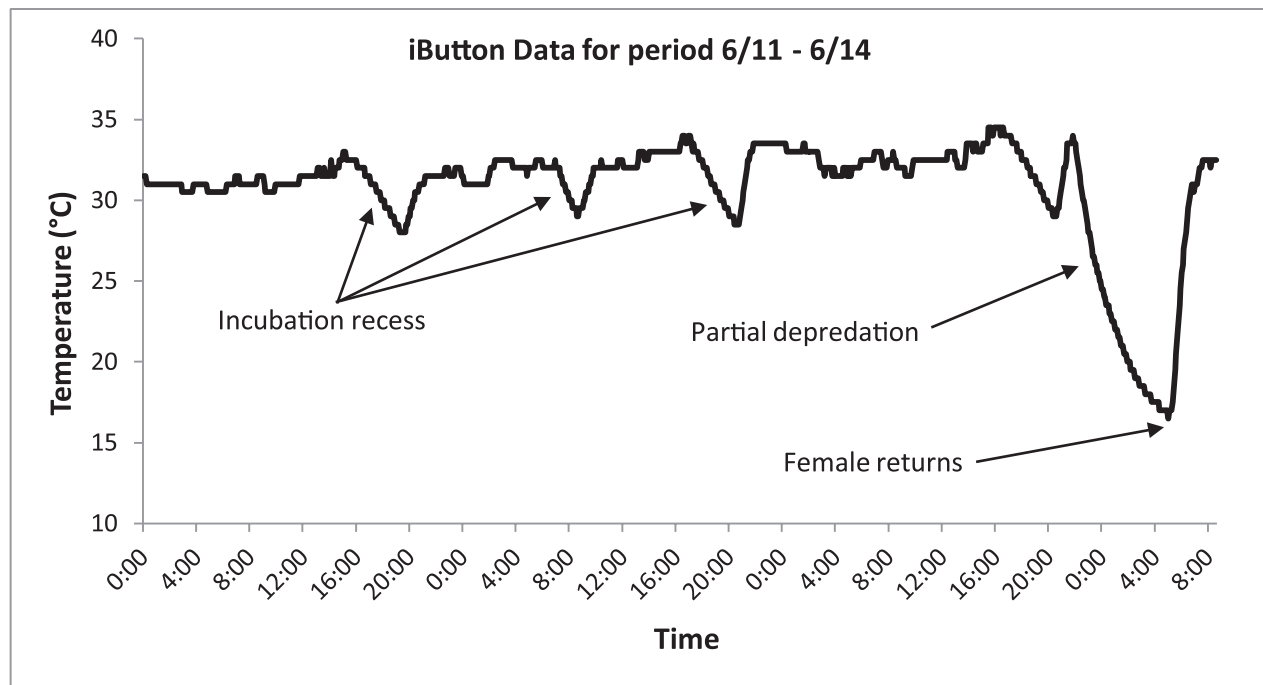
FIGURE 1.   An example of an output graph from Rhythm/Raven, showing several days of patterns of nest incubation by a Gadwall at Grizzly Island, California.

number of recesses per day for those nests for which there was sufficient data ($n = 13$) was 1.7 ± 0.1 per 24-hr period.

We modeled the effect of species, nest age, Julian date, (centered) clutch size, mean daily temperature, minimum daily temperature, and pd-status on the durations of incubation shifts and recesses. In Table 1, we show the top four models, ranked by AIC_c score, and report model-averaged parameter estimates in Table 2. Somewhat surprisingly, the duration of incubation shifts was not significantly affected by

species, nest age, Julian date, or mean ambient temperature, with all parameters bounding zero at the 95% level (Table 2). After a partial depredation, however, hens significantly *increased* the time spent on the nest. Our model indicates that after a partial depredation hens increased the average duration of incubation shifts by more than 200 min (Table 2), which contradicts our original hypothesis that parental investment should decline following partial clutch loss. Our results also show that females generally incubate in longer shifts when incubating larger clutches. However, females increase investment more when the magnitude of clutch

TABLE 1.   Top four models of duration incubation shift, ranked by AIC_c score. Nest was included as a random effect in all models.

Model parameters	ΔAIC_c	AIC model weight
Species + age + date + pd-status + clutch size + pd × clutch size + mean temperature + minimum temperature	0.0[a]	0.692
Species + age + pd-status + clutch size + pd × clutch size + mean temperature + minimum temperature	1.9	0.258
Species + pd-status + clutch size + pd × clutch size + mean temperature + minimum temperature	5.3	0.047
Species + age + date + pd-status + clutch size + pd × clutch size + minimum temperature	11.6	0.002

[a]$AIC_c = 7600.3$.

TABLE 2.   Model-averaged coefficient estimates for parameters affecting duration of incubation shifts. Clutch size has been centered. Parameters for which $P < 0.05$ are shown in **bold**.

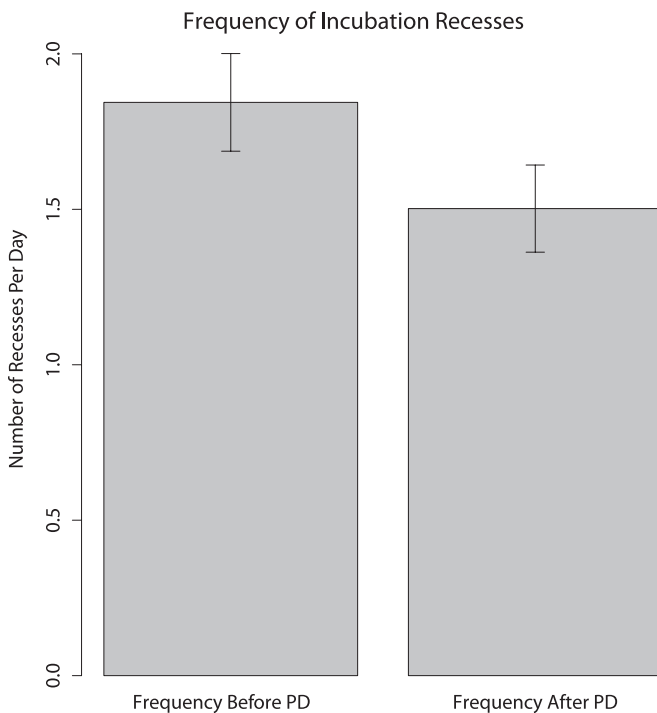| Parameter	Estimate	SE	z-value	$P(>|z|)$
(Intercept)	**886.56**	**338.09**	**2.62**	**<0.01**
Species (Mallard)	−129.64	109.53	1.18	0.24
Age	−2.97	4.49	0.66	0.51
Date	−1.44	2.60	0.55	0.58
Pd-status	**204.90**	**78.16**	**2.62**	**<0.01**
Clutch size	**75.20**	**32.36**	**2.32**	**0.02**
Minimum temperature	**31.60**	**11.26**	**2.81**	**<0.01**
Mean temperature	−16.49	10.17	1.62	0.10
Clutch size × pd-status	**−93.03**	**36.69**	**2.54**	**0.01**

Frequency of Incubation Recesses

FIGURE 2.   The mean number of incubation recesses per day (with standard error bars) before and after partial depredation of Mallard and Gadwall nests at Grizzly Island, California. After partial clutch loss, hens took significantly fewer incubation recesses per day.

reduction following a partial depredation is greater (significant pd × clutch size interaction term, Table 2). Finally, we found that higher minimum daily temperatures were associated with longer incubation shifts.

The only variable influencing the duration of incubation recesses was the daily minimum temperature (model-averaged estimate: 7.82 ± 2.59, $P < 0.01$), which indicates that females took longer recesses when minimum temperatures were warmer. Neither partial clutch loss nor any other variable had an effect on the duration of incubation recesses (all $P > 0.05$). However, when we examined how the frequency of incubation recesses changed after a partial depredation, we found that hens took fewer recesses per day after a partial depredation ($\mu_{before} = 1.84 \pm 0.16$, $\mu_{after} = 1.50 \pm 0.14$, $t = -3.97$, $P < 0.01$) (Fig. 2). Again, contrary to our original hypothesis, hens appeared to be increasing parental investment by reducing the number of recesses per day following partial clutch loss.

DISCUSSION

We found no support for the expected-benefits hypothesis, which predicts that hens should decrease the level of parental investment after the expected reproductive benefits are reduced. On the contrary, we found that after partial clutch loss hens *increased* the level of parental investment in a nest and, furthermore, increases in investment were larger when the reduction of the clutch was greater. After a partial depredation, hens also decreased the number of recesses per day and increased the duration of incubation shifts. This is somewhat consistent with the Skutch hypothesis: hens reduced the activity level at the nest, but, interestingly, they did not increase the duration of incubation recesses. Therefore, this increased investment in the nest almost certainly imposes a body-condition cost on the hen as she spends less time foraging (Afton and Paulus 1992). We found that incubation rhythms depended on the ambient daily minimum temperature: warmer nights were associated with longer shifts and recesses. It is presumably optimal to incubate the clutch for as long as possible during the night: thus we suggest that warmer nights allow the female to remain on the nest longer because they may impose less of an energetic demand on her. Our finding that females take longer recesses on warmer nights tends to support the thermal-inertia hypothesis because clutches would cool more slowly when nightly temperatures are higher. More relevant to this study, the thermal-inertia hypothesis also predicts that hens should take shorter, more frequent recesses after a clutch reduction in order to maintain quickly cooling small clutches at developmental temperatures, yet we found no support for this hypothesis.

In summary, while we found the most support for the Skutch hypothesis, we remain skeptical of the underlying assumption that reduced activity at the nest attenuates the risk of predation of nests of the ducks we studied. The primary predators on Grizzly Island are skunks that locate nests at night via olfaction; therefore, it seems unlikely that hens would alter levels of visible activity at the nest in response to these types of predators. Furthermore, the Skutch hypothesis predicts that females should also take longer recesses to recoup energy reserves, which was not supported by our data. So, given that females spend more time on the nest (longer incubation shifts, less frequent recesses) yet do not change the duration of their recesses, the question remains: why might females invest more in a nesting attempt when the expected benefits have been reduced?

One possibility is that we are studying an unusual subset of birds; many hens abandon the nest after a partial depredation, so perhaps those that remain are unusual in some way. Dabbling ducks often lay replacement clutches after the first is destroyed (Johnson et al. 1992), so it may be adaptive for many hens to abandon a depredated nest and initiate a new clutch elsewhere. The results of Ackerman et al. (2003) suggest that the non-abandoned nests we studied should be high-value nests with large expected benefits. Indeed, all of our nests were partially depredated at least 16 days into incubation and tended to lose not more than half the clutch. In addition to having nests of moderate to high value, the hens we studied that chose to remain

with the partially depredated nest may have been unable to lay a replacement clutch for physiological (e.g., poor body condition; Hansson et al. 2003) or environmental reasons (e.g., too late in the season; Alisauskas and Ankney 1992, Bluhm 1992). Therefore, perhaps their optimal strategy is to "make the best of a bad situation" by remaining with the current nest. However, even if these birds are "stuck" with the current clutch of eggs, that does not explain why the level of investment *increases* following a partial depredation.

One explanation is that smaller clutches are generally less costly to incubate (Thomson et al. 1998) (though they tend to cool more quickly), so females in poor condition may benefit by remaining with the current clutch and using less energy to incubate the remaining eggs. This agrees with our result showing that females increase investment more when clutch-size reductions are greater; perhaps females with drastically reduced clutches are able to remain on the nest longer while paying the same energetic cost as females whose clutches were reduced less.

A second explanation for why females increase parental investment following partial clutch loss is that they are attempting to increase their levels of nest defense against known predators—a form of Bayesian updating in response to changes in information about predation risk. Several studies have shown that birds can alter their investment strategies as they obtain information about predation risk (Fontaine and Martin 2006, Dassow et al. 2012). At the nests we studied, partial depredation provides females with an index of predation risk if predators are more likely to return to a partially depredated nest. If predators are known to be in the area, females should increase the amount of time they spend on the nest *if two critical assumptions are met*: (1) the female's presence reduces predation risk through camouflage (Kreisinger and Albrecht 2008) or physical deterrence (Opermanis 2004), and (2) predators pose little risk of mortality to females. We believe that the predator community at our study site satisfies these assumptions.

The primary nest predator at our study site at Grizzly Island is the Striped Skunk, a small mesopredator that during the nesting season forages within a relatively static home range (Larivière and Messier 1998, 2000). Because skunks forage primarily through olfactory cues (Nams 1997), the presence of an incubating hen probably provided little benefit of (visual) concealment. However, a 1- to 2-kg skunk not only poses little threat to the hen herself (at our study site, females are much less likely to be killed on the nest, McLandress et al. 1996), but the physical presence of a 1-kg Mallard hen may be enough to deter and/or physically block a skunk from depredating the eggs in the nest. This may be especially true if duck nests are depredated only incidentally as skunks search for their preferred prey, small mammals (Larivière and Messier 2001). Therefore, the optimal parental investment strategy for hens at our study site, given the initial decision to remain with a partially depredated nest, may be to increase nest defense in response to known predation risk from predators that pose little risk to the hen.

This situation stands in stark contrast to that commonly found in the prairie pothole region of North America, where the majority of the continent's dabbling ducks breed. While our study site is devoid of foxes (McLandress et al. 1996, Ackerman and Eadie 2003), on the prairies the Red Fox (*Vulpes vulpes*) has historically been an important nest predator. Foxes pose a considerable threat to both eggs and incubating hens (Klett et al. 1988, Johnson et al. 1989, Pasitschniak-Arts and Messier 1995), making the decision to remain with a partially depredated nest especially risky. We suspect that in this region fewer hens would choose to remain with a partially depredated clutch and those that do would reduce parental investment to ameliorate the mortality risk posed by foxes.

Despite a decrease in expected benefits, hens at our study site increased parental investment in nest defense following a partial depredation. While the optimal strategy for many birds may be to abandon the nest and lay a replacement clutch elsewhere (Ackerman and Eadie 2003), the optimal investment strategy for those birds electing to remain with the current nest may be to increase nest defense against known predators to ensure at least *some* (though reduced) reproductive benefits from a clutch. Further research is needed to determine whether, as we suspect, this investment strategy depends on the local predator community and the risk of mortality it poses to the incubating female.

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