



Cues for investment: nest desertion in response to partial clutch depredation in dabbling ducks

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(Received 24 June 2002; initial acceptance 8 November 2002;
final acceptance 24 January 2003; MS. number: A9389)

Parents may use several cues to assess offspring value; however, most studies of parental care have examined only one or a few cues, and often in just a single species. This approach has produced conflicting results, with limited generality, and it remains unclear which cues animals use to adjust parental care. We examined nest desertion in response to natural clutch reductions by predators to determine which of several cues female dabbling ducks use to assess offspring value. Of 3562 duck nests monitored between 1996 and 2001, 30.5% of clutches were partially depredated, of which females deserted 37.7%. Mallard, *Anas platyrhynchos* ($N=754$) and gadwall, *A. strepera* ($N=221$) females were more likely to stay with proportionately larger remaining clutch sizes, older clutches and nests with eggs missing rather than with eggshell evidence of depredation. The proportion of the clutch remaining had the greatest influence on the likelihood that a nest would be deserted, indicating that females assess clutch value primarily using the remaining clutch size relative to the initial clutch size. On average, females deserted nests when 37–45% of the clutch remained (3–4 eggs) and continued to provide care when 73–75% of the clutch remained (6–7 eggs). Nest initiation date was not an important cue influencing desertion. Northern pintail, *A. acuta* ($N=33$) females behaved similarly, although we could not determine which of several cues relating to clutch size they used because multiple models fit the data well. Our results indicate that several factors influence clutch value and that ducks are able to use multiple cues to finely adjust their level of parental care following partial clutch depredation.

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Parental investment theory predicts that parental behaviours are selected to maximize lifetime reproductive success, based on a trade-off between present and future reproduction (Williams 1966; Trivers 1972; Sargent & Gross 1985; Coleman & Gross 1991). Parents should provide care for their current offspring only when the benefits of doing so outweigh the potential reduction in the parents' survival and future reproduction (Coleman & Gross 1991; Stearns 1992). Thus, parents should adjust their level of care when subjected to adverse conditions such as predation. For many birds, nest depredation is the single most important factor affecting fitness (Ricklefs 1969), and investigations of parental care decisions made under the risk of predation have contributed substantially

to our understanding of parental investment theory (review by Montgomerie & Weatherhead 1988). Despite these advances, however, there still are few clear tests of the proximate cues animals use to determine when to continue or curtail parental care under natural conditions.

Two approaches have predominated in studies of parental investment decisions made under the risk of predation. The first approach examines risk-taking behaviour by parents in defence of their offspring. Numerous studies have used behavioural observations of nest defence against model predators or humans simulating the risk of predation (Montgomerie & Weatherhead 1988). However, methodological constraints may limit the utility of such approaches; for example, live predators and model predators (or humans) often do not elicit comparable behavioural responses from parents (Knight & Temple 1986). A second approach has been to examine offspring desertion in response to a change in the expected benefit of current reproduction (e.g. partial

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clutch loss; review by Székely et al. 1996). Desertion of young provides an unambiguous measure of parental investment because parents either stay with their offspring and continue to provide care, or desert and terminate care before the offspring are capable of surviving independently (Fujioka 1989). Because parents derive no benefit from offspring they have deserted, but may still benefit from poorly defended young, analyses of offspring desertion may provide a more powerful test of the predictions of parental investment theory than nest defence behaviour. Offspring desertion as a life-history strategy has been reported in a variety of taxa (e.g. Tait 1980; Robertson & Roitberg 1998; Jennions & Polakow 2001), and especially in birds (Székely et al. 1996); however, until recently, it has been used infrequently to assess the cues animals use to adjust their level of parental care (Eadie & Lyon 1998; Jennions & Polakow 2001; Verboven & Tinbergen 2002).

Offspring desertion often occurs in birds during the clutch stage in response to nest depredation (Ricklefs 1969, 1977). Although nest depredation typically is viewed as an all-or-none event, many nests are depredated only partially (especially in the Anatidae; Grand & Flint 1997; Larivière & Messier 1997; Ackerman et al. 2003) and the remaining clutch often is successful when the parent continues to provide care (Ackerman 2002a). The decision to desert a partially depredated clutch therefore has important implications for a parent's fitness (Székely et al. 1996). Because partial clutch depredation occurs throughout the nesting season, at all stages of incubation (i.e. clutch ages), and results in various remaining clutch sizes (Ackerman et al. 2003), it provides a unique opportunity with which to assess the cues used to adjust parental care under natural conditions.

Several recent studies of offspring desertion have investigated cues used to adjust parental care, but most studies have focused on only one or a few cues in a single species (e.g. Pöysä et al. 1997; Eadie & Lyon 1998; Gendron & Clark 2000; Jennions & Polakow 2001; Verboven & Tinbergen 2002). Montgomerie & Weatherhead (1988) concluded more than a decade ago that there are a multitude of factors that should affect parental care, and studies focusing on only a few variables could lead to flawed or incomplete interpretations. Hence, it is not surprising that recent studies have produced conflicting results and there has been little consensus on the cues used to assess offspring value and to adjust parental care (e.g. contrast Pöysä et al. 1997 and Eadie & Lyon 1998).

In this paper, we first discuss several cues available for parents to assess offspring value after a naturally occurring perturbation, partial clutch depredation. We then investigate which of these cues are used by dabbling ducks to adjust parental care. Nesting dabbling ducks are ideal subjects for studying parental behaviours under the risk of predation. Only one sex (females) provides parental care, so offspring desertion by the parent invariably results in nest failure. Moreover, females and their nests are subjected to intense predation (Cowardin et al. 1985; Klett et al. 1988; Greenwood et al. 1995), but offspring that survive to hatching are precocial and require less parental care (Oring & Saylor 1992). Therefore, it is likely

that selection has acted strongly to shape female parental behaviours during the nesting stage.

Cues for Parental Investment

The cues that females could use to assess the value of a partially depredated clutch can be broadly grouped into three categories: (1) attributes relating to the remaining clutch size after the depredation event, (2) the timing of the depredation event, both within the reproductive attempt and nesting season and (3) physical evidence remaining after the depredation event (e.g. broken eggs or eggshells). Parental characteristics (e.g. body condition, age, experience) also may influence the value of current offspring relative to future reproductive prospects (Montgomerie & Weatherhead 1988; Székely et al. 1996), but we do not consider these here.

Clutch size attributes

Clutch size attributes include the absolute remaining clutch size (Eadie & Lyon 1998), the remaining clutch size relative to the initial clutch size (i.e. the proportion of the clutch remaining; Galvani & Coleman 1998) and clutch mortality rate (Carlisle 1982; Pöysä et al. 1997). Although these cues contain similar information and typically are highly correlated, it is unclear which of these cues parents actually use. The clutch size hypothesis predicts that females will be more likely to stay with (absolute) larger remaining clutch sizes because they have a larger reproductive value, and will desert when the benefit of staying is less than that of deserting (Grafen & Sibly 1978; Eadie & Lyon 1998). The relative value hypothesis predicts that females will be more likely to stay with proportionately larger remaining clutch sizes, even when the absolute remaining clutch sizes are identical, because the value of a clutch of a given size depends on the reproductive potential of the parent (Montgomerie & Weatherhead 1988; Galvani & Coleman 1998; Robertson & Roitberg 1998). According to this hypothesis, parents with lower current fecundity have a lower potential to reproduce in the future (i.e. lower residual reproductive value due to, for example, individual quality or body size; see Galvani & Coleman 1998; Robertson & Roitberg 1998). For example, the size of replacement clutches birds lay after desertion often is positively correlated with the original clutch size (Arnold 1993; Verboven & Tinbergen 2002). Therefore, the current reproductive value of a clutch reduced to a given size will be greater for the parent that laid fewer eggs initially (and therefore has a larger proportion of the clutch remaining). Finally, the brood success hypothesis predicts that females will be more likely to stay with clutches suffering lower amounts of past mortality, because past mortality indicates future survival prospects of offspring within a clutch (Carlisle 1982; Pöysä et al. 1997). Thus, clutches suffering higher mortality in the past have a lower reproductive value because they have lower future survival prospects. Mortality rate not only incorporates information about clutch size (i.e. the number of depredated offspring), but also the timing of the depredation event within the

Table 1. A summary of hypotheses and related cues addressing how parents adjust their level of care in response to partial clutch loss to predators

Hypothesis	Prediction: parents are more likely to stay with:	References
Clutch size attributes		
Clutch/brood size	(Absolute) larger clutches	Grafen & Sibly 1978; Eadie & Lyon 1998; Montgomerie & Weatherhead 1988
Relative value	Proportionally larger clutches	Montgomerie & Weatherhead 1988; Galvani & Coleman 1998; Robertson & Roitberg 1998
Clutch/brood success	Clutches experiencing lower past mortality	Carlisle 1982; Pöysä et al. 1997
Timing of depredation		
Clutch/brood age	Clutches partially depredated late in incubation	Montgomerie & Weatherhead 1988
Past investment	Clutches partially depredated late in incubation	Sargent & Gross 1985; Curio 1987; Coleman & Gross 1991
Duckling survival	Clutches initiated earlier in the nesting season	Montgomerie & Weatherhead 1988
Renesting potential	Clutches initiated later in the nesting season	Montgomerie & Weatherhead 1988
Physical evidence of depredation		
Eggshell evidence	Clutches with missing eggs rather than clutches with eggshell evidence of depredation	This study

reproductive attempt. Therefore, clutch mortality rate often is correlated with both attributes of clutch size and the timing of depredation. Few studies have clearly distinguished between these alternatives.

Timing of depredation

Females might also use information about the timing of the depredation event to adjust parental care because both the stage of incubation at the time of depredation and the timing of the reproductive attempt during the breeding season can affect offspring value. For example, females may use incubation stage as a cue to adjust parental care because nests partially depredated late in incubation presumably are more valuable for several reasons. The clutch age hypothesis predicts that females will be more likely to stay with clutches that are partially depredated late in incubation because the probability of survival to hatching for older offspring is greater than that for younger offspring (Montgomerie & Weatherhead 1988). The past investment hypothesis also predicts that females will be more likely to stay with clutches that are partially depredated late in incubation because a parent's past investment is larger in older than younger offspring. Prior investment in offspring can reduce a parent's ability to reproduce in the future; hence, past investment can increase the value of current offspring relative to future reproductive prospects (Curio 1987; Coleman & Gross 1991). Females might also use nest initiation date as a cue to adjust parental care because the timing of the reproductive attempt during the nesting season can affect the prospects for both duckling survival and renesting potential. The duckling survival hypothesis predicts that females will be more likely to stay with partially depredated nests that were initiated early in the breeding

season (Montgomerie & Weatherhead 1988), because the survival of early-hatched broods typically is higher than that of later hatched broods (Orthmeyer & Ball 1990; Rotella & Ratti 1992; Dzus & Clark 1998; Guyn & Clark 1999). Conversely, the renesting potential hypothesis predicts that females will be more likely to stay with partially depredated nests that were initiated late in the breeding season, because renesting potential is greater earlier than later in the nesting season and later-nesting females therefore have lower prospects for renesting (Montgomerie & Weatherhead 1988).

Physical evidence of depredation

In cases of partial clutch depredation, a female also could use the physical evidence remaining (i.e. eggshells) after the depredation event to forecast future depredation events (either to themselves or the remaining eggs) and, thus, assess the relative reproductive value of the current offspring. For example, the probability of survival for the remaining eggs in nests with eggshell evidence (remaining near the nest site) may be lower than that for partially depredated nests with eggs missing because eggshells may provide olfactory or visual cues for nest predators that could lead to subsequent depredation events (Olson & Rohwer 1998; Larivière 1999).

These hypotheses and associated cues are summarized in Table 1. We investigate the use of each of these cues in female dabbling ducks by examining nest desertion resulting from partial clutch loss. We use large samples of partial clutch depredations occurring naturally over a 6-year period in three species to simultaneously evaluate the use of multiple cues and their generality among species.

METHODS

Study Area and Species

We conducted our study at the Grizzly Island Wildlife Area in the Suisun Marsh of California, U.S.A. (38°14'N, 121°97'W; see [McLandress et al. 1996](#) for a detailed description of the area). The Suisun Marsh is a large (~34 000 ha) brackish estuary at the downstream end of the Sacramento–San Joaquin Delta that drains into the San Francisco Bay. The Grizzly Island Wildlife Area contains roughly 2000 ha of wetlands and 1600 ha of uplands. Between 1996 and 2001, we searched 190–256 ha of upland habitat each year for duck nests, totaling 1316 ha. We examined a broad range of representative habitats within the study area, although areas searched were not randomly selected because of logistical constraints.

Five species of dabbling ducks (Anatidae, Tribe Anatini) nest on the ground within these upland habitats; mallard, *Anas platyrhynchos*, are the most numerous, followed by gadwall, *A. strepera*, northern pintail, *A. acuta*, cinnamon teal, *A. cyanoptera*, and northern shoveler, *A. clypeata*. We excluded cinnamon teal and northern shoveler nests from analyses because of the small sample sizes of partially depredated nests ($N=12$ and 7 , respectively). Female dabbling ducks lay one egg per day and begin the incubation period (24–26 days) approximately when the full clutch is laid (8–10 eggs; [Klett et al. 1986](#); [Afton & Paulus 1992](#)). The precocial offspring leave the nest within 24–48 h of hatching and are able to walk, swim and feed on their own as soon as they leave the nest ([Afton & Paulus 1992](#)). Renesting is common in dabbling ducks if the initial nest has been destroyed ([Bellrose 1976](#); [Swanson et al. 1986](#)).

Nest Searching and Monitoring Techniques

Waterfowl nest search procedures were designed following [Klett et al. \(1986\)](#), and were modified following [McLandress et al. \(1996\)](#) for this study site. Nest searches were initiated in early April and continued until July to ensure finding both early- and late-nesting ducks ([McLandress et al. 1996](#)). The date of nest initiation was calculated by subtracting the age of the nest when found (i.e. the number of eggs when found plus the incubation stage when found) from the date the nest was discovered ([Klett et al. 1986](#)). Each field was searched four to five times at 3-week intervals until no new nests were found. Nest searches began at least 2 h after sunrise and were finished by 1400 hours to avoid missing nests due to morning and afternoon nest breaks by females ([Caldwell & Cornwell 1975](#); [Gloutney et al. 1993](#)). Nest searches were conducted using a 50-m nylon rope strung between two slow-moving, all-terrain vehicles. Tin cans containing stones to generate noise were attached at 1.5-m intervals along the length of the rope. The rope was dragged through the vegetation, causing females to flush from their nests, thus enabling observers to locate nests by searching a restricted area. Each nest was marked with a 2-m bamboo stake placed 4 m north of the nest bowl,

and a shorter stake placed just south of the nest bowl, level with the vegetation height. Each nest was revisited on foot once every 7 days, the stage of embryo development was determined by candling ([Weller 1956](#)), and clutch size and nest fate (hatched, destroyed, or deserted) were recorded. After each visit, we covered the eggs with nest materials (i.e. down and contour feathers from the nest), as the female would have done before leaving for an incubation recess. Nests that were deserted on the day they were found or partially depredated before they were found were excluded from all analyses ([Klett et al. 1986](#)). We also excluded nests that were disturbed by investigators, such as nests that were altered by clutch size manipulations ([Ackerman & Eadie 2003](#)) and those damaged by nest searching or egg-handling procedures.

Partial Clutch Depredation

We considered a nest to be partially depredated when the clutch size was reduced between consecutive investigator visits and at least one egg was still intact in the nest bowl. We categorized partially depredated nests as having either eggs missing or destroyed (i.e. broken eggs or eggshell fragments; hereafter 'eggshell evidence') present within 3 m of the nest. Nests with eggshell evidence also may have had some eggs that were missing, whereas nests categorized as eggs missing had no eggshell evidence. The date of partial depredation was estimated as the midpoint between discovery of the depredation event and the preceding visit (maximum error of ± 3.5 days), and the incubation stage at the time of the partial depredation event was defined as the number of days the eggs had been incubated before that date. If the partial depredation event caused the female to desert the nest, we also used the arrested development of the embryo in the remaining eggs to determine the stage of incubation at which the depredation event occurred (via candling; [Weller 1956](#)). Nests in which all eggs were nonviable (i.e. infertile, addled, or contained dead embryos) were excluded from analyses because we were unable to determine the incubation stage (i.e. the age of the clutch when partial depredation occurred) via candling. Mortality rate was calculated as the number of depredated eggs divided by the age of the clutch (i.e. the number of eggs laid plus the incubation stage; [Klett et al. 1986](#)) when the partial depredation event occurred.

Parental Care Decisions

Nest desertion from partial clutch loss was determined from multiple clues, including female absence, egg temperature, down placement and arrested embryonic development ([Klett et al. 1986](#)). A nest was not considered deserted if we flushed the female from the nest after the partial depredation event (desertion generally occurs within 24 h of clutch loss; [Armstrong & Robertson 1988](#); J. T. Ackerman, personal observations). If we were uncertain of a nest's status (deserted or active), we revisited it within 7 days to confirm that the female had either deserted or stayed with the reduced clutch. If we were still

uncertain of the nest's status after the partial depredation event (e.g. if we found the nest further depredated upon our revisit), we excluded it from analyses. To avoid the confounding effects that multiple partial clutch depredations may have on a female's decision to desert, only the first partial clutch loss caused by a predator in a series of partial depredations was used in analyses. Additionally, nests with evidence that the female had been killed during the partial depredation event were excluded from analyses of nest desertion.

Statistical Analysis

We considered multiple models incorporating differing combinations of six cues (i.e. proportion of the clutch remaining, absolute number of eggs remaining, clutch mortality rate, incubation stage, eggshell evidence and Julian nest initiation date) and used Akaike's Information Criterion (AIC; Burnham & Anderson 1998) to select the most parsimonious model for the probability of staying with a partially depredated clutch. Three cues (i.e. clutch size attributes; Table 1) contain similar information about clutch size and we expected them to be highly correlated. Therefore, we built three sets of models a priori to distinguish between these clutch size attributes: those incorporating (1) the proportion of the clutch remaining (2) the absolute number of eggs remaining, and (3) clutch mortality rate. Each set of models considered a single clutch size attribute alone and with all possible combinations of the other predictor variables (i.e. incubation stage, eggshell evidence and Julian nest initiation date). We excluded incubation stage from models that contained mortality rate because mortality rate already contained information about the timing (during the reproductive attempt) of the partial clutch depredation event and we expected these variables to be highly correlated. Additionally, we built a fourth set of models that excluded clutch size attributes. These models considered each remaining variable alone and in combination with the others. For each model, we calculated log-likelihood values using multiple logistic regression.

We considered the model with the smallest Akaike Information Criterion ($AIC = -2(\log\text{-likelihood}) + 2(\text{number of fitted parameters})$) to be the most parsimonious. This approach often performs better than restricting the final model to those variables with statistically significant effects in the full model, especially for observational data (Burnham & Anderson 1998; Anderson et al. 2000). For northern pintail, we used a second-order AIC, which is necessary for small sample sizes: $AIC_c = -2(\log\text{-likelihood}) + 2K(N/N - K - 1)$, where K is the number of fitted parameters and N is the sample size (Burnham & Anderson 1998; Anderson et al. 2000). We calculated the AIC (or AIC_c) differences between the best model and all other models considered for each species ($\Delta_i = AIC_i - \text{minimum AIC}$) to determine the relative ranking of each candidate model; models for which $\Delta_i \leq 2$ have substantial support and were considered for biological importance (Burnham & Anderson 1998; Anderson et al. 2000). We also calculated Akaike weights ($w_i = \exp[-\Delta_i/2] / \sum \exp[-\Delta_i/2]$) to assess the weight of evidence that the selected

model was the actual Kullback–Leibler best model in the set of models considered (Burnham & Anderson 1998; Anderson et al. 2000).

In addition to determining the most parsimonious model for the set of cues used to adjust parental care, we wanted to assess the relative importance of each cue in the selected model. Among our sets of models, there was partial model redundancy that we could not correct for using differential priors (Burnham & Anderson 1998) because each variable appeared an unequal number of times (Table 2). Thus, had we used Akaike weights to assess the relative importance of the variables in the selected model, the variables that appeared in models most often (e.g. eggshell evidence) would have diluted the absolute strength of evidence for variables that appeared fewer times (e.g. proportion of clutch remaining; Burnham & Anderson 1998). Although Anderson et al. (2001) do not recommend mixing analysis paradigms, lacking an alternative, we resorted to traditional statistical approaches (i.e. multiple logistic regression) to gain further insight into which of the cues provided the greatest predictive power. Multiple logistic regression also allowed us to calculate odds ratios to relate the likelihood of staying with an incremental increase in each of the cues while controlling for other variables (see Table 3). For the few other statistical tests, we log transformed mortality rate data to meet the assumption of normality in parametric tests and used nonparametric tests, corrected for ties, when the data could not be transformed to meet this assumption. Means ± 1 SD are presented and all tests are two tailed.

RESULTS

Of 3562 duck nests monitored between 1996 and 2001, 754 mallard, 221 gadwall and 33 northern pintail nests were suitable for analyses of parental response to natural clutch reductions. Partial clutch loss by predators was common in all species and years; on average, 30.5% of duck nests were partially depredated at least once. Predators depredated 3.0 ± 2.2 mallard, 3.9 ± 2.5 gadwall and 3.5 ± 2.6 northern pintail eggs per clutch, or $37.1 \pm 26.0\%$, $36.8 \pm 25.3\%$ and $39.9 \pm 25.9\%$ of clutches, respectively, during the initial partial depredation event. On average, females deserted 37.7% of these partially depredated nests.

Model Selection

Clutch size attributes were strong predictors of a female's decision to desert after partial clutch depredation. In general, univariate analyses indicated that the probability of a female staying with a nest increased with the absolute size of the remaining clutch (logistic regression: mallard: Wald $\chi^2_1 = 159.91$, $N = 754$, $P < 0.0001$; gadwall: Wald $\chi^2_1 = 50.36$, $N = 221$, $P < 0.0001$; northern pintail: Wald $\chi^2_1 = 8.18$, $N = 33$, $P = 0.004$) and the proportion of the clutch remaining (logistic regression: mallard: Wald $\chi^2_1 = 178.01$, $N = 754$, $P < 0.0001$; gadwall: Wald $\chi^2_1 = 58.93$, $N = 221$, $P < 0.0001$; northern pintail: Wald $\chi^2_1 = 9.25$, $N = 33$,

Table 2. Summary of a priori candidate models considered for the cues used to adjust parental care, the number of model parameters (K), Akaike's Information Criterion (AIC), the difference between the candidate model and the best model (Δ_i) and Akaike weights (w_i) for each duck species

Model	K	AIC			Δ_i			w_i		
		Mallard	Gadwall	Northern pintail	Mallard	Gadwall	Northern pintail	Mallard	Gadwall	Northern pintail
Models with the proportion of the clutch remaining (pN)										
pN	2	756.90	205.76	30.62	162.70	24.34	5.28	0.00	0.00	0.02
pN+Inc	3	664.92	194.72	26.89	70.72	13.30	1.55	0.00	0.00	0.11
pN+Shells	3	651.68	188.00	29.53	57.48	6.58	4.19	0.00	0.02	0.03
pN+Date	3	758.84	203.64	32.67	164.64	22.22	7.33	0.00	0.00	0.01
pN+Inc+Shells	4	594.20	181.42	29.09	0.00	0.00	3.75	0.51	0.52	0.04
pN+Inc+Date	4	665.18	194.26	29.41	70.98	12.84	4.07	0.00	0.00	0.03
pN+Shells+Date	4	652.24	187.42	32.13	58.04	6.00	6.79	0.00	0.03	0.01
pN+Inc+Shells+Date	5	594.30	181.76	31.74	0.10	0.34	6.40	0.48	0.44	0.01
Models with the number of eggs remaining (N)										
N	2	781.80	223.74	30.12	187.60	42.32	4.78	0.00	0.00	0.02
N+Inc	3	708.64	217.60	27.01	114.44	36.18	1.67	0.00	0.00	0.10
N+Shells	3	658.36	202.14	28.89	64.16	20.72	3.55	0.00	0.00	0.04
N+Date	3	776.40	225.00	32.55	182.20	43.58	7.21	0.00	0.00	0.01
N+Inc+Shells	4	611.82	199.20	28.95	17.62	17.78	3.61	0.00	0.00	0.04
N+Inc+Date	4	695.16	219.52	29.07	100.96	38.10	3.73	0.00	0.00	0.04
N+Shells+Date	4	655.18	203.78	31.37	60.98	22.36	6.03	0.00	0.00	0.01
N+Inc+Shells+Date	5	603.16	201.12	31.22	8.96	19.70	5.88	0.01	0.00	0.01
Models with mortality rate (MR)										
MR	2	690.74	209.38	25.34	96.54	27.96	0.00	0.00	0.00	0.23
MR+Shells	3	615.42	194.32	26.85	21.22	12.90	1.51	0.00	0.00	0.11
MR+Date	3	692.72	208.06	27.75	98.52	26.64	2.41	0.00	0.00	0.07
MR+Shells+Date	4	617.34	194.18	29.45	23.14	12.76	4.11	0.00	0.00	0.03
Models without clutch size attributes										
Inc	2	941.48	293.96	40.88	347.28	112.54	15.54	0.00	0.00	0.00
Shells	2	752.48	242.52	29.52	158.28	61.10	4.18	0.00	0.00	0.03
Date	2	1003.88	291.14	47.64	409.68	109.72	22.30	0.00	0.00	0.00
Inc+Shells	3	721.42	243.56	30.57	127.22	62.14	5.23	0.00	0.00	0.02
Inc+Date	3	942.66	291.40	42.49	348.46	109.98	17.15	0.00	0.00	0.00
Shells+Date	3	754.12	241.78	31.77	159.92	60.36	6.43	0.00	0.00	0.01
Inc+Shells+Date	4	721.80	243.12	32.85	127.60	61.70	7.51	0.00	0.00	0.01

pN=Proportion of the clutch remaining, N=absolute number of eggs remaining, MR=mortality rate, Inc=incubation stage, Shells=eggshell evidence, Date=Julian nest initiation date. Values of Δ_i and w_i for the most parsimonious model for each species are in boldface italics, and for models that have substantial support are in bold (i.e. $\Delta_i \leq 2$). For northern pintail, we used a second-order AIC (AICc), which is necessary for small sample sizes.

$P=0.002$), and decreased with clutch mortality rate (logistic regression: mallard: Wald $\chi^2=165.32$, $N=754$, $P<0.0001$; gadwall: Wald $\chi^2=47.96$, $N=221$, $P<0.0001$; northern pintail: Wald $\chi^2=8.25$, $N=33$, $P=0.004$). However, as expected, these clutch size attributes were highly correlated in each species (Pearson correlation or Spearman rank correlation: all $|r_{752}|$, $|r_{219}|$, $|r_{31}|$ or $r_s \geq 0.77$, $N_{\text{mallard}}=754$, $N_{\text{gadwall}}=221$, $N_{\text{pintail}}=33$, $P<0.0001$). Therefore, we felt it was appropriate to use the separate candidate models for each clutch size attribute, combined with the other potential cues, which we developed a priori (see Methods). Incubation stage and mortality rate also were correlated in each species (Pearson correlation: all $r < -0.31$, $P<0.001$); therefore, it was appropriate to exclude incubation stage from models containing mortality rate.

For mallard and gadwall, the most parsimonious model contained the proportion of the clutch remaining, incubation stage and eggshell evidence (Table 2). A second

candidate model containing these variables and Julian nest initiation date also provided a good fit to the data (Table 2). For northern pintail, mortality rate provided the most parsimonious model, but candidate models using the other clutch size attributes also fit the data well and could not be ruled out (i.e. the models with $\Delta_i \leq 2$ shown in bold in Table 2).

Evaluation of Cues

We used multiple logistic regression to determine the relative importance of the cues in the selected models. For mallard and gadwall, we present the full model including Julian nest initiation date. The proportion of the clutch remaining had the largest influence on a female's decision to desert (Table 3). The probability of staying increased with the proportion of the clutch remaining in a similar manner for each species, and increased most rapidly when between 40% and 60% of the clutch

Table 3. Multiple logistic regression of the most parsimonious model describing the probability of staying with a partially depredated clutch

Species/model's predictor variables	Coefficient±SE	Wald χ^2_1	P	Odds ratio (95% CI) for staying with each incremental increase in variable
Mallard (N=754)				
Proportion of clutch remaining	5.04±0.50	102.82	<0.0001	1.66 (1.50, 1.82) per 0.10 pN
Eggshell evidence: missing	1.80±0.21	70.27	<0.0001	6.02 (3.96, 9.16) with eggs missing
Incubation stage	0.13±0.02	52.59	<0.0001	1.14 (1.10, 1.18) per 1 day later in Inc
Nest initiation date	0.01±0.01	1.89	0.17	1.01 (1.00, 1.02) per 1 day later in Date
Gadwall (N=221)				
Proportion of clutch remaining	6.31±0.97	42.23	<0.0001	1.88 (1.55, 2.27) per 0.10 pN
Eggshell evidence: missing	1.38±0.39	12.67	<0.001	3.97 (1.86, 8.50) with eggs missing
Incubation stage	0.09±0.03	7.09	<0.01	1.10 (1.02, 1.17) per 1 day later in Inc
Nest initiation date	-0.02±0.02	1.65	0.20	0.98 (0.95, 1.01) per 1 day later in Date*

For mallard and gadwall, the full models selected using Akaike's Information Criterion are shown. For northern pintail, many candidate models fit the data substantially well ($\Delta_i \leq 2$), therefore no model was chosen. Odds ratios give the likelihood of staying with each incremental increase in the variable. For example, mallards were 1.66 times more likely to stay with each 0.10 increase in the proportion of the clutch remaining and 6.02 times more likely to stay when eggs were missing than when there was eggshell evidence of partial clutch depredation. pN=Proportion of the clutch remaining, Inc=incubation stage, Date=Julian nest initiation date.

*The negative coefficient and odds ratio of less than 1.00 indicates that gadwall were slightly more likely to desert (not stay) per 1 day later in nest initiation date.

remained (Fig. 1). The average size of deserted clutches was three to four eggs or when 37–45% of the clutch remained, whereas the average size of clutches for females that stayed was six to seven eggs or when 73–75% of the clutch remained (Table 4). The absolute remaining clutch size in nests where females stayed differed between species (ANOVA: $F_{2,625}=8.52$, $P=0.0002$), but the proportion of the clutch remaining was similar (Kruskal–Wallis test: $H_2=0.69$, $P=0.71$; Table 4).

Although the proportion of the clutch remaining was the most important cue influencing whether females deserted, additional cues were used (Table 3). Incubation stage influenced the likelihood that the female would desert; in each species, the probability of a female staying with a partially depredated clutch gradually increased with incubation stage (Fig. 1). We detected a relatively small influence of Julian nest initiation date on a female's decision to desert a partially depredated clutch (Table 3, Fig. 2), despite this variable being included in a candidate model that provided a good fit to the data (Table 2).

Eggshell evidence of partial clutch depredation located near the nest site further influenced a female's decision (Table 3). Partially depredated nests frequently had eggs missing (56.1% of partially depredated nests) without other evidence, such as broken eggs and eggshells, that would indicate disturbance by a predator. Nests with eggs missing lost fewer eggs to predators (mallard: 2.1 ± 1.6 eggs, $N=416$; gadwall: 2.5 ± 2.0 eggs, $N=131$; northern pintail: 1.9 ± 1.7 eggs, $N=18$) than nests with eggshell remains (mallard: 4.1 ± 2.3 eggs, $N=338$, Mann–Whitney U test: $U=33987$, $P<0.0001$; gadwall: 4.7 ± 2.6 eggs, $N=89$, $U=2962$, $P<0.0001$; northern pintail: 5.3 ± 2.3 eggs, $N=15$, $U=20$, $P<0.0001$). After controlling for other variables, mallard and gadwall females were more likely to stay with partially reduced clutches when eggs were missing than when eggshell evidence was found within 3 m of the nest (Table 3). We also examined whether the probability of survival to hatching (when the female stayed) for the remaining eggs in nests with eggshell

evidence was lower than that for nests with eggs missing while controlling for the other variables (i.e. proportion of the clutch remaining, incubation stage, Julian nest initiation date). The probability of successfully hatching one or more of the remaining eggs in partially depredated nests was greater for gadwall nests when eggs were missing than when there was eggshell evidence (logistic regression: Wald $\chi^2_1=8.01$, $N=134$, $P=0.005$), but we did not detect a difference for mallard (logistic regression: Wald $\chi^2_1=1.98$, $N=469$, $P=0.16$) or northern pintail (logistic regression: Wald $\chi^2_1<0.01$, $N=21$, $P=0.99$) nests.

DISCUSSION

We used 6 years of data for three species to simultaneously examine multiple cues that parents might use to assess offspring value and to evaluate the generality of these cues among species. Nest depredation at our study site, as in most waterfowl breeding habitats, was high (review by Sargeant & Raveling 1992): mallard nest success averaged 17.9% (yearly range 5.6–33.6%; California Waterfowl Association, unpublished data) and 30.5% of all duck nests were partially depredated. Under such conditions, selection should act strongly to shape parental behaviours in response to partial clutch loss. Our results demonstrate that female dabbling ducks use a variety of cues to adjust their level of parental care, indicating that multiple factors influence clutch value. Information about the remaining clutch size, timing of predation and physical evidence at the nest all were used by females to make parental care decisions. Mallard, gadwall and northern pintail females behaved similarly and were more likely to stay with proportionately larger remaining clutch sizes (Fig. 1), older clutches (Fig. 1) and nests where eggs were missing instead of nests with eggshell evidence of depredation (Table 3). Nest initiation date had little influence on a female's decision to desert (Fig. 2). We consider the relevance of each of these cues below.

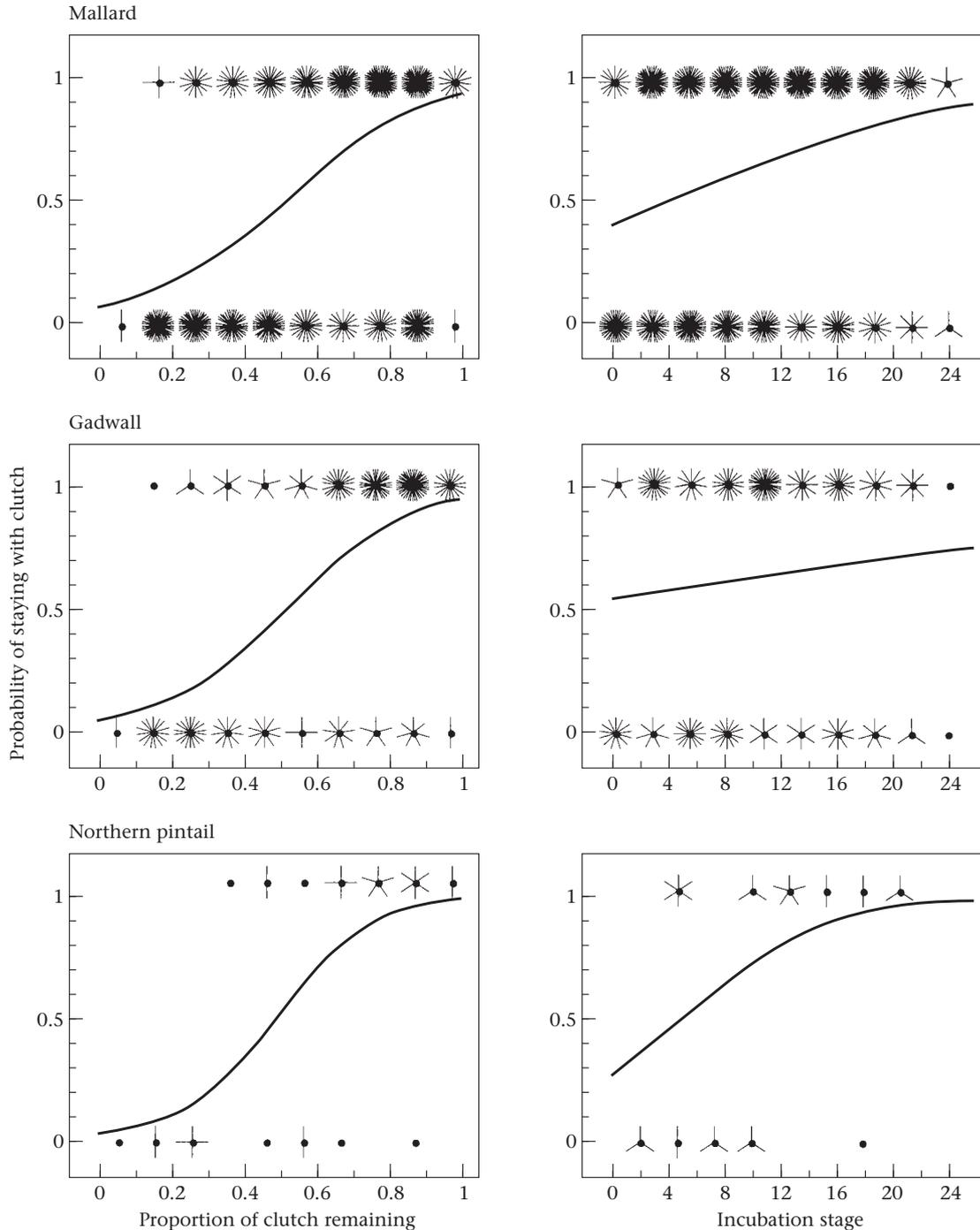


Figure 1. The influence of the proportion of the clutch remaining and incubation stage on a female's decision to stay with a partially depredated clutch ($Y=1$) or desert ($Y=0$) for mallard ($N=754$), gadwall ($N=221$) and northern pintail ($N=33$). The lines indicate the logistic regressions between the proportion of the clutch remaining, or incubation stage, and the probability that a female would stay with a partially depredated clutch. The equations for the proportion of the clutch remaining were: mallard: $p(\text{stay})=1-(1/(1+\exp(-2.78+5.35\times\text{proportion of clutch remaining})))$; gadwall: $p(\text{stay})=1-(1/(1+\exp(-3.22+6.14\times\text{proportion of clutch remaining})))$; northern pintail: $p(\text{stay})=1-(1/(1+\exp(-3.83+7.72\times\text{proportion of clutch remaining})))$. The equations for the incubation stage at partial clutch depredation were: mallard: $p(\text{stay})=1-(1/(1+\exp(-0.46+0.10\times\text{incubation stage})))$; gadwall: $p(\text{stay})=1-(1/(1+\exp(0.13+0.04\times\text{incubation stage})))$; northern pintail: $p(\text{stay})=1-(1/(1+\exp(-1.07+0.20\times\text{incubation stage})))$. Each leg of a star indicates one data point.

Clutch Size Attributes

Each clutch size variable we examined (Table 1) predicted a female's decision to desert a partially depredated

nest when considered individually. Desertion rates have been shown to increase with the severity of the experimental clutch or brood reduction in a variety of taxa (Armstrong & Robertson 1988; Beissinger 1990; Winkler

Table 4. The number of eggs remaining and the percentage of clutch remaining in nests where the female stayed or deserted after partial clutch depredation

Species	Initial clutch size	Stay			Desert		
		Number of eggs remaining	Percentage of the clutch remaining	N	Number of eggs remaining	Percentage of the clutch remaining	N
Mallard	8.3±1.6	6.3±2.0	74.1±17.4	469	3.7±2.3	45.2±25.9	285
Gadwall	9.3±1.7	7.1±2.2	75.3±17.0	138	3.9±2.7	42.3±25.5	83
Northern pintail	8.6±1.7	6.3±2.0	73.1±15.9	21	3.1±1.9	37.4±24.6	12

Means are reported ±1 SD.

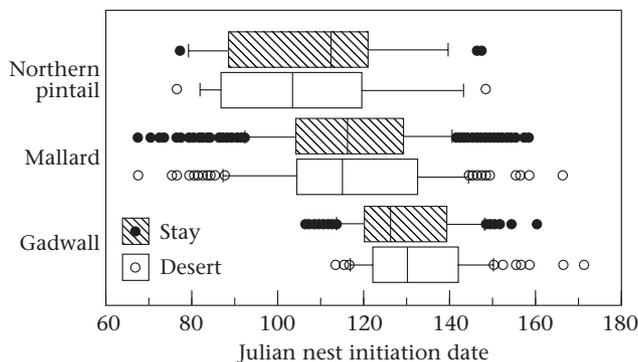


Figure 2. Box plots of partially depredated clutches for which the females stayed or deserted in relation to Julian nest initiation date for mallard (stay: $N=469$; desert: $N=285$), gadwall (stay: $N=138$; desert: $N=83$) and northern pintail (stay: $N=21$; desert: $N=12$).

1991; Delehanty & Oring 1993; Eadie & Lyon 1998; Jennions & Polakow 2001; Verboven & Tinbergen 2002). Thus, parents clearly do respond to some attribute of clutch size. However, the question remains, which of these cues is the best predictor of parental behaviour? Using AIC model selection criteria, we found that the most parsimonious models for mallard and gadwall were those that included the proportion of the clutch remaining (Table 2). Therefore, if two clutches had different initial clutch sizes but each was reduced to the same clutch size, the female with a proportionately larger remaining clutch was more likely to stay. This result is consistent with the relative value hypothesis (Montgomerie & Weatherhead 1988; Galvani & Coleman 1998; Robertson & Roitberg 1998). Females may use the proportion of the clutch remaining to modify their parental care because the value of a clutch of any given size depends on the reproductive potential of the parent. If reproductive potential varies among individuals, then similar clutch sizes represent different proportions of an individual's lifetime reproductive success. The proportion of the clutch remaining rather than the absolute remaining clutch size would be a better predictor of a female's decision to desert because it more accurately reflects the value of the reduced clutch relative to each individual's lifetime reproductive success.

In our study, the probability of a female staying with a partially reduced clutch increased most rapidly when 40–60% of the clutch remained (Fig. 1), and there was no

difference between species in the proportion of the clutch remaining when females stayed with partially depredated nests (Table 4). After controlling for other variables known to influence parental care, mallard and gadwall were 1.66 and 1.88 times more likely to stay with each 10% increase in the proportion of the original clutch remaining (Table 3). Similarly, Armstrong & Robertson (1988) found that nest desertion rates for blue-winged teal, *A. discors*, were correlated with the proportion of the clutch removed, such that females deserted all nests in which more than 65% of the clutch had been experimentally removed and stayed with all nests with less than a 30% reduction in clutch size. Likewise, Eadie & Lyon (1998) found that the desertion threshold for Barrow's goldeneyes, *Bucephala islandica*, was approximately four ducklings (40–60% of the brood remained). Székely et al. (1996) compiled data for waterfowl and other avian species and found a similar pattern between nest desertion and the proportion of the clutch remaining. These data suggest that, across species, the decision to desert is influenced by a general clutch size threshold based on the proportion of the clutch remaining.

How might females detect the proportion of the clutch remaining? Levels of prolactin, an essential reproductive hormone for incubation patch formation and maintenance in birds (Goldsmith & Williams 1980; Hall & Goldsmith 1983; Hall 1991), are dependent on tactile stimulation received at the incubation patch in ducks, not on visual stimuli (Hall & Goldsmith 1983; Hall 1987a). Reduced prolactin levels (within 24 h) caused by partial clutch loss are associated with nest desertion in mallards (Hall 1987a, b). Thus, the relative change in incubation patch stimulation after partial clutch loss may be the key sensory mechanism by which ducks assess the proportion of the clutch remaining, and thereby adjust their level of parental care.

We found some evidence that northern pintail also may use mortality rate to adjust their level of parental care, consistent with the brood success hypothesis (Carlisle 1982; Pöysä et al. 1997). However, we also found substantial support for models containing other clutch size cues (i.e. the proportion of the clutch remaining and absolute number of eggs remaining) and could not rule them out (Table 2). These ambiguous results probably are a consequence of low statistical power for this species, and larger sample sizes will be required to determine more precisely which clutch size attribute northern

pintails use to assess offspring value. Few other studies have addressed the brood success hypothesis, although Pöysä et al. (1997) found that maternal effort in common goldeneye ducks, *B. clangula*, is modified according to the previous mortality of the brood.

Timing of Depredation

Females also used incubation stage as a cue to adjust their parental care. In each species, the probability of a female staying with a partially depredated clutch increased with the stage of incubation (Fig. 1). After controlling for other variables known to influence parental care, mallard and gadwall were 1.14 and 1.10 times more likely to stay with each additional day spent in incubation (Table 3). Similarly, Wilson's phalarope, *Phalaropus tricolor*, and great tit, *Parus major*, parents are more likely to desert clutches experimentally reduced to similar sizes earlier than later in incubation (Delehanty & Oring 1993; Verboven & Tinbergen 2002). Using measures of nest defence, Forbes et al. (1994) for mallards, Mallory et al. (1998) for common goldeneyes and hooded mergansers, *Lophodytes cucullatus*, and Sjöberg (1994) for Canada geese, *Branta canadensis*, showed that females take greater risks as incubation proceeds. Both the direction and gradual form of the relationship between the probability of staying and incubation stage (Fig. 1) are consistent with parental investment theory. For example, parental care should increase gradually throughout the incubation period because the probability of the eggs surviving until hatching increases as they age (Montgomerie & Weatherhead 1988). In addition, a parent's past investment is greater in older than younger offspring and, because past investment devalues future reproduction, the value of the current clutch relative to future reproductive prospects increases with offspring age (Curio 1987; Coleman & Gross 1991). Whether parents adjust their care according to offspring age or past investment is unclear (Table 1), and can only be uncoupled experimentally (sensu Sargent & Gross 1985). We did so elsewhere for mallards by experimentally reducing clutches at two different incubation stages such that they had equivalent expected benefits (i.e. clutch size weighted by age) but differed in the amount of past investment. Contrary to the past investment hypothesis, our results indicated that the increase in parental care with incubation stage observed in mallards was due to increasing expected benefits as clutches age rather than to the influence of past investment on the prospects for future reproduction (Ackerman & Eadie 2003).

Nest initiation date had a relatively small influence on whether a female deserted a partially depredated clutch (Table 3, Fig. 2; also see Forbes et al. 1994; Guinness et al. 2001). Mallards were slightly more likely (odds ratio=1.01), whereas gadwall were slightly less likely (odds ratio=0.98), to stay with partially depredated clutches with each subsequent day in the season that the nests were initiated (Table 3). Because duckling survival in early-hatched broods typically is higher than in later-hatched broods (Orthmeyer & Ball 1990; Rotella & Ratti

1992; Dzus & Clark 1998; Guyn & Clark 1999), females might be expected to invest more in nests initiated early in the season. However, re-nesting potential is greater earlier in the nesting season than later, and so it also could be argued that females should invest more heavily in later nests when their prospects for re-nesting are low (Montgomerie & Weatherhead 1988). These effects may cancel each other and could explain why there is such limited evidence of an influence of nest initiation date on parental investment behaviour in birds (Montgomerie & Weatherhead 1988).

Physical Evidence of Depredation

Interestingly, we found that eggshell evidence of partial clutch depredation located near the nest site also influenced a female's decision to desert (Table 3), a phenomenon that has not been reported previously. After controlling for other variables, mallard and gadwall females were 6.02 and 3.97 times more likely to stay with partially depredated clutches when eggs were missing than when eggshell evidence was found at the nest site (Table 3). There are at least four potential explanations for this response. First, eggshells remaining near the nest may be the cue indicating that a partial depredation event has occurred. Hence, a female encountering eggshell remains at her nest has confirmation of a depredation event, whereas a depredation event resulting in missing eggs may go unnoticed. This explanation seems unlikely considering that the probability that a female will desert a nest with missing eggs depends, in large part, on the proportion of the clutch remaining (Table 3). Thus, females appear to be capable of assessing the proportion of offspring remaining even when there is no eggshell evidence of depredation.

Second, if females consume eggshells or remove them from nest sites (Larivière & Walton 1998; Pietz & Granfors 2000), observers would not find eggshell evidence even though the partial depredation event resulted in eggshells being left near the nest. In this scenario, a female might decide to stay with a partially depredated nest and then remove the eggshells, thus biasing the data to appear as if females were more likely to stay when eggs were missing. Evidence for eggshell consumption or removal by female ducks is scarce (Larivière & Walton 1998) and the majority of partially depredated nests in this study resulted in missing eggs, suggesting that most of the nests with eggs missing probably depict the actual evidence remaining after depredation.

Third, eggshell evidence may indicate the type of predator responsible for nest depredation. Parental behaviours such as nest defence often are specific to the type of predator (Montgomerie & Weatherhead 1988; Ghalambor & Martin 2000). Possibly, female ducks use encounters with nest predators and the evidence remaining after a partial depredation attempt to assess not only the benefit of the remaining clutch but also the cost (i.e. the probability of survival) to themselves. Fewer eggs were lost from nests when the only evidence of partial clutch depredation was missing eggs. Although it is difficult to

determine the identity of predators from nest remains (review by Larivière 1999), perhaps smaller predators (i.e. gopher snakes, *Pituophis melanoleucus*, and common ravens, *Corvus corax*) were responsible. Small predators pose little threat to the survival of a nesting female, whereas larger predators of duck nests at our study site (i.e. coyotes, *Canis latrans*, striped skunks, *Mephitis mephitis*, racoons, *Procyon lotor*; Ackerman 2002b) might return and injure or kill the incubating female. Female dabbling ducks have high mortality rates during the breeding season (up to 40%), largely because of their increased vulnerability to predators while incubating nests (Sargeant et al. 1984; Sargeant & Raveling 1992; Greenwood et al. 1995). The cost to the female of continuing to provide care for a partially depredated clutch with eggshell evidence may be substantially larger than that for a nest with eggs missing. Thus, female dabbling ducks may adjust their level of parental care not only according to the benefit of a reduced clutch, but also to the perceived cost to themselves (also see Guinness et al. 2001). This explanation is plausible only if female ducks can use the evidence remaining at nests after partial clutch depredation to reliably identify classes of predators (i.e. threatening or nonthreatening to incubating females).

Fourth, in contrast to partially depredated nests with eggs missing, eggshells may provide olfactory or visual cues for nest predators that could lead to subsequent depredation events (Olson & Rohwer 1998; Larivière 1999). In this case, the probability of survival to hatching for the remaining eggs in nests with eggshell evidence may be lower than that for nests with eggs missing. Females therefore may use eggshell evidence to forecast future depredation events, and would be more likely to stay with nests when eggs are missing because the expected benefit of the remaining eggs is greater than in nests with eggshell evidence. We found some support for this explanation; the probability of successfully hatching (when females stayed) was greater for partially depredated gadwall, but not mallard, nests when eggs were missing than when there was eggshell evidence. Manipulative experiments will be necessary to fully understand why females are more likely to stay with partially depredated nests when eggs are missing than when there is eggshell evidence remaining near the nest site.

Our results underscore the importance of considering multiple cues simultaneously when investigating how animals adjust parental care, especially when trying to separate cues containing correlated information (such as the brood size and brood success hypotheses; Table 1). Failure to do so may have contributed to apparent discrepancies between studies in which only one or a few cues were considered (e.g. Pöysä et al. 1997; Eadie & Lyon 1998). Clearly, several factors influence the reproductive value of a partially depredated clutch, and female dabbling ducks appear to be able to use multiple cues to finely adjust their level of parental care. Our results and those of others (Armstrong & Robertson 1988; Forbes et al. 1994; Sjöberg 1994; Mallory et al. 1998) further suggest that several waterfowl species use similar cues to assess offspring value and adjust parental care while under the risk of predation.

Acknowledgments

This research was funded by the California Waterfowl Association, Delta Waterfowl Foundation, Dennis G. Raveling Endowment and a University of California (UC) Davis Jastro-Shields Scholarship. J. T. Ackerman was supported by a UC Davis Ecology Graduate Group Block Grant, UC Davis Zolk Fellowship in Ecology, Dennis G. Raveling Scholarship, Stockton Sportsmen's Club Scholarship and the Dennis G. Raveling Endowment. We thank A. Blackmer, R. Colvis, D. Consoli, D. Cross, J. DiSalvo, C. Haffner, P. Jackson, L. Kanemoto, S. Kenady, R. Kurth, K. Lamb, E. Matchett, C. Reyes and R. Roninger for field assistance, and the California Department of Fish and Game staff at the Grizzly Island Wildlife Area for logistical support. We also thank Elliot Matchett for data entry, Julie Yee and Neil Willits for much statistical advice, and Alexis Blackmer, Tamás Székely, Dirk Van Vuren and an anonymous referee for helpful comments on the manuscript.

References

- Ackerman, J. T. 2002a. From individuals to populations: the direct and indirect effects of predation on waterfowl nest success. Ph.D. thesis, University of California, Davis.
- Ackerman, J. T. 2002b. Of mice and mallards: positive indirect effects of coexisting prey on waterfowl nest success. *Oikos*, **99**, 469–480.
- Ackerman, J. T. & Eadie, J. M. 2003. Current versus future reproduction: an experimental test of parental investment decisions using nest desertion by mallards (*Anas platyrhynchos*). *Behavioral Ecology and Sociobiology*, **54**, 264–273.
- Ackerman, J. T., Eadie, J. M., Loughman, D. L., Yarris, G. S. & McLandress, M. R. 2003. The influence of partial clutch depredation on duckling production. *Journal of Wildlife Management*, **67**, 576–587.
- Afton, A. D. & Paulus, S. L. 1992. Incubation and brood care. In: *Ecology and Management of Breeding Waterfowl* (Ed. by B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec & G. L. Krapu), pp. 62–108. Minneapolis: University of Minnesota Press.
- Anderson, D. R., Burnham, K. P. & Thompson, W. L. 2000. Null hypothesis testing: problems, prevalence, and an alternative. *Journal of Wildlife Management*, **64**, 912–923.
- Anderson, D. R., Link, W. A., Johnson, D. H. & Burnham, K. P. 2001. Suggestions for presenting the results of data analyses. *Journal of Wildlife Management*, **65**, 373–378.
- Armstrong, T. & Robertson, R. J. 1988. Parental investment based on clutch value: nest desertion in response to partial clutch loss in dabbling ducks. *Animal Behaviour*, **36**, 941–943.
- Arnold, T. W. 1993. Factors affecting re-nesting in American coots. *Condor*, **95**, 273–281.
- Beissinger, S. R. 1990. Experimental brood manipulations and the monoparental threshold in snail kites. *American Naturalist*, **136**, 20–38.
- Bellrose, F. C. 1976. *Ducks, Geese and Swans of North America*. Harrisburg, Pennsylvania: Stackpole.
- Burnham, K. P. & Anderson, D. R. 1998. *Model Selection and Inference: a Practical Information-theoretic Approach*. New York: Springer-Verlag.
- Caldwell, P. J. & Cornwell, G. W. 1975. Incubation behavior and temperatures of the mallard duck. *Auk*, **92**, 706–731.

- Carlisle, T. R. 1982. Brood success in variable environments: implications for parental care allocation. *Animal Behaviour*, **30**, 824–836.
- Coleman, R. M. & Gross, M. R. 1991. Parental investment theory: the role of past investment. *Trends in Evolution and Ecology*, **6**, 404–406.
- Cowardin, L. M., Gilmer, D. S. & Schaiffer, C. W. 1985. Mallard recruitment in the agricultural environment of North Dakota. *Wildlife Monographs*, **92**, 1–37.
- Curio, E. 1987. Animal decision-making and the 'Concorde fallacy'. *Trends in Evolution and Ecology*, **2**, 148–152.
- Delehanty, D. J. & Oring, L. W. 1993. Effect of clutch size on incubation persistence in male Wilson's phalaropes (*Phalaropus tricolor*). *Auk*, **110**, 521–528.
- Dzus, E. H. & Clark, R. G. 1998. Brood survival and recruitment of mallards *Anas platyrhynchos* in relation to wetland density and hatching date. *Auk*, **115**, 311–318.
- Eadie, J. M. & Lyon, B. E. 1998. Cooperation, conflict, and crèching behavior in goldeneye ducks. *American Naturalist*, **151**, 397–408.
- Forbes, M. R. L., Clark, R. G., Weatherhead, P. J. & Armstrong, T. 1994. Risk-taking by female ducks: intra- and interspecific tests of nest defense theory. *Behavioral Ecology and Sociobiology*, **34**, 79–85.
- Fujioka, M. 1989. Mate and nest desertion in colonial little egrets. *Auk*, **106**, 292–302.
- Galvani, A. P. & Coleman, R. M. 1998. Do parental convict cichlids of different sizes value the same brood number equally? *Animal Behaviour*, **56**, 541–546.
- Gendron, M. & Clark, R. G. 2000. Factors affecting brood abandonment in gadwalls (*Anas strepera*). *Canadian Journal of Zoology*, **78**, 327–331.
- Ghalambor, C. K. & Martin, T. E. 2000. Parental investment strategies in two species of nuthatch vary with stage-specific predation risk and reproductive effort. *Animal Behaviour*, **60**, 263–267.
- Gloutney, M. L., Clark, R. G., Afton, A. D. & Huff, G. J. 1993. Timing of nest searches for upland nesting waterfowl. *Journal of Wildlife Management*, **57**, 597–601.
- Goldsmith, A. R. & Williams, D. M. 1980. Incubation in mallards (*Anas platyrhynchos*): changes in plasma levels of prolactin and luteinizing hormone. *Journal of Endocrinology*, **86**, 371–379.
- Grafen, A. & Sibly, R. 1978. A model of mate desertion. *Animal Behaviour*, **26**, 645–652.
- Grand, J. B. & Flint, P. L. 1997. Productivity of nesting spectacled eiders on the lower Kashunuk River, Alaska. *Condor*, **99**, 926–932.
- Greenwood, R. J., Sargeant, A. B., Johnson, D. H., Cowardin, L. M. & Shaffer, T. L. 1995. Factors associated with duck nest success in the prairie pothole region of Canada. *Wildlife Monographs*, **128**, 1–57.
- Gunness, M. A., Clark, R. G. & Weatherhead, P. J. 2001. Counter-intuitive parental investment by female dabbling ducks in response to variable habitat quality. *Ecology*, **82**, 1151–1158.
- Guyn, K. L. & Clark, R. G. 1999. Factors affecting survival of northern pintail ducklings in Alberta. *Condor*, **101**, 369–377.
- Hall, M. R. 1987a. External stimuli affecting incubation behavior and prolactin secretion in the duck (*Anas platyrhynchos*). *Hormones and Behavior*, **21**, 269–287.
- Hall, M. R. 1987b. Nesting success in mallards after partial clutch loss by predators. *Journal of Wildlife Management*, **51**, 530–533.
- Hall, M. R. 1991. Endocrinological and behavioral changes associated with the onset of incubation in the duck. *Physiology & Behavior*, **50**, 311–316.
- Hall, M. R. & Goldsmith, A. R. 1983. Factors affecting prolactin secretion during breeding and incubation in the domestic duck (*Anas platyrhynchos*). *General and Comparative Endocrinology*, **49**, 270–276.
- Jennions, M. D. & Polakow, D. A. 2001. The effect of partial brood loss on male desertion in a cichlid fish: an experimental test. *Behavioral Ecology*, **12**, 84–92.
- Klett, A. T., Duebbert, H. F., Faanes, C. A. & Higgins, K. F. 1986. Techniques for studying nest success of ducks in upland habitats in the prairie pothole region. *U.S. Fish and Wildlife Service Resource Publication*, **158**, 1–24.
- Klett, A. T., Shaffer, T. L. & Johnson, D. H. 1988. Duck nest success in the prairie pothole region. *Journal of Wildlife Management*, **52**, 431–440.
- Knight, R. L. & Temple, S. A. 1986. Methodological problems in studies of avian nest defence. *Animal Behaviour*, **34**, 561–566.
- Larivière, S. 1999. Reasons why predators cannot be inferred from nest remains. *Condor*, **101**, 718–721.
- Larivière, S. & Messier, F. 1997. Characteristics of waterfowl nest depredation by the striped skunk, *Mephitis mephitis*: can predators be identified from nest remains? *American Midland Naturalist*, **137**, 393–396.
- Larivière, S. & Walton, L. R. 1998. Eggshell removal by duck hens following partial nest depredation by striped skunk. *Prairie Naturalist*, **30**, 183–185.
- McLandress, M. R., Yarris, G. S., Perkins, A. E. H., Connelly, D. P. & Raveling, D. G. 1996. Nesting biology of California mallards. *Journal of Wildlife Management*, **60**, 94–107.
- Mallory, M. L., McNicol, D. K. & Walton, R. A. 1998. Risk-taking by incubating common goldeneyes and hooded mergansers. *Condor*, **100**, 694–701.
- Montgomerie, R. D. & Weatherhead, P. J. 1988. Risks and rewards of nest defence by parent birds. *Quarterly Review of Biology*, **63**, 167–187.
- Olson, R. & Rohwer, F. C. 1998. Effects of human disturbance on success of artificial duck nests. *Journal of Wildlife Management*, **62**, 1142–1146.
- Oring, L. W. & Saylor, R. D. 1992. The mating systems of waterfowl. In: *Ecology and Management of Breeding Waterfowl* (Ed. by B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec & G. L. Krapu), pp. 190–213. Minneapolis: University of Minnesota Press.
- Orthmeyer, D. L. & Ball, I. J. 1990. Survival of mallard broods on Benton Lake National Wildlife Refuge in north-central Montana. *Journal of Wildlife Management*, **54**, 62–66.
- Pietz, P. J. & Granfors, D. A. 2000. Identifying predators and fates of grassland passerine nests using miniature video cameras. *Journal of Wildlife Management*, **64**, 71–87.
- Pöysä, H., Virtanen, J. & Milonoff, M. 1997. Common goldeneyes adjust maternal effort in relation to prior brood success and not current brood size. *Behavioral Ecology and Sociobiology*, **40**, 101–106.
- Ricklefs, R. 1969. An analysis of nestling mortality in birds. *Smithsonian Contribution to Zoology*, **9**, 1–48.
- Ricklefs, R. 1977. On the evolution of reproductive strategies in birds: reproductive effort. *American Naturalist*, **111**, 453–478.
- Robertson, I. C. & Roitberg, B. D. 1998. Duration of parental care in pine engraver beetles: why do large males care less? *Behavioral Ecology and Sociobiology*, **43**, 379–386.
- Rotella, J. J. & Ratti, J. T. 1992. Mallard brood movements and wetland selection in southwestern Manitoba. *Journal of Wildlife Management*, **56**, 508–515.
- Sargeant, A. B. & Raveling, D. G. 1992. Mortality during the breeding season. In: *Ecology and Management of Breeding Waterfowl* (Ed. by B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec & G. L. Krapu), pp. 396–422. Minneapolis: University of Minnesota Press.
- Sargeant, A. B., Allen, S. H. & Eberhardt, R. T. 1984. Red fox predation on breeding ducks in mid-continent North America. *Wildlife Monographs*, **89**, 1–41.

- Sargent, R. C. & Gross, M. R.** 1985. Parental investment decision rules and the Concorde fallacy. *Behavioral Ecology and Sociobiology*, **17**, 43–45.
- Sjöberg, G.** 1994. Factors affecting nest defence in female Canada geese *Branta canadensis*. *Ibis*, **136**, 129–135.
- Stearns, S. C.** 1992. *The Evolution of Life Histories*. Oxford: Oxford University Press.
- Swanson, G. A., Shaffer, T. L., Wolf, J. F. & Lee, F. B.** 1986. Renesting characteristics of captive mallards on experimental ponds. *Journal of Wildlife Management*, **50**, 32–38.
- Székely, T., Webb, J. N., Houston, A. I. & McNamara, J. M.** 1996. An evolutionary approach to offspring desertion in birds. *Current Ornithology*, **13**, 271–330.
- Tait, D. E. N.** 1980. Abandonment as a reproductive tactic: the example of grizzly bears. *American Naturalist*, **115**, 800–808.
- Trivers, R. L.** 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man* (Ed. by B. Campbell), pp. 136–179. Chicago: Aldine.
- Verboven, N. & Tinbergen, J. M.** 2002. Nest desertion: a trade-off between current and future reproduction. *Animal Behaviour*, **63**, 951–958.
- Weller, M. W.** 1956. A simple field candler for waterfowl eggs. *Journal of Wildlife Management*, **20**, 111–113.
- Williams, G. C.** 1966. Natural selection, costs of reproduction, and a refinement of Lack's principle. *American Naturalist*, **100**, 687–690.
- Winkler, D. W.** 1991. Parental investment decision rules in tree swallows: parental defense, abandonment, and the so-called Concorde Fallacy. *Behavioral Ecology*, **2**, 133–142.