



Parental Investment Theory and Nest Defence by Imperial Shags: Effects of Offspring Number, Offspring Age, Laying Date and Parent Sex

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Abstract

Nest defence is a common form of parental care employed by birds to improve the survival of their offspring. Theory predicts that parents should adjust their nest defence according to the value of the brood at stake, defending more intensively broods with high survival and reproductive prospects. We evaluated the influence of offspring number, offspring age, laying date and parent sex on nest-defence intensity (NDI) of the Imperial Shag *Phalacrocorax atriceps*, a sexually dimorphic seabird with seasonal decline in offspring survival and very limited re-nesting potential. We also evaluated whether NDI was correlated within pairs and whether NDI of both members of the pair was correlated with incubation and breeding success. To elicit defensive behaviour, we simulated predation attempts using a Kelp Gull *Larus dominicanus* model. As predicted by theory, NDI was positively correlated with the number of offspring in the nest and offspring age. NDI during chick rearing was higher than that at early and late incubation, while no differences were found between incubation stages. Contrary to our prediction, we did not find differences in NDI according to laying date. NDI for males was higher than females, while NDI was also positively correlated within pairs. NDI was not statistically related to incubation or breeding success. These results suggest that other factors, such as laying date or parental quality and age, play a much larger role in determining the outcome and productivity of a nesting attempt. Our results provide partial support for parental investment theory; while parental defence increased with brood value according to offspring number and age, parental defence was not related to laying date, a factor strongly affecting offspring survival and recruitment probabilities in this species.

Introduction

Defence of eggs and nestlings at the nest is a common form of parental care employed by birds to improve the survival of their offspring. Several studies have shown that parents who defend their nests more vigorously suffer lower nest predation (Anderson et al. 1980; Greig-Smith 1980; Knight & Temple

1986a; Tryjanowski & Gołowski 2004) and enjoy higher offspring recruitment (Kontiainen et al. 2009) than less vigorous defenders. The study of intraspecific variation in nest defence provides a fertile arena to test hypotheses derived from life history theory (Stearns 1992), in general, and parental investment theory (Trivers 1972; Dawkins & Carlisle 1976; Maynard Smith 1977), in particular. Theory predicts that

animals should adjust their parental investment in relation to the value of the offspring to maximise future net benefits (Trivers 1972; Dawkins & Carlisle 1976). Therefore, parents would invest in nest defence according to the reproductive value of the offspring at stake, defending more intensively clutches or broods with high survival and reproductive prospects.

The value of a clutch or brood to the parents could be determined by variables such as the number of offspring in the nest, offspring age and date of clutch initiation (reviewed in Montgomerie & Weatherhead 1988). The value of the clutch or brood increases with offspring number because there is a higher probability that more offspring will reach independence and reproduce. Therefore, parents should defend large broods more vigorously than small broods (Andersson et al. 1980; Greig-Smith 1980; Montgomerie & Weatherhead 1988; Redondo 1989). Also, from the time an egg is laid until the chick fledges, the reproductive value of that offspring increases because the probability of survival until reproduction is higher in older offspring than in younger ones (Dawkins & Carlisle 1976; Boucher 1977; Andersson et al. 1980). Several theoretical (Andersson et al. 1980; Montgomerie & Weatherhead 1988; Redondo 1989) and empirical (Greig-Smith 1980; Wallin 1987; Tryjanowski & Goławski 2004; Redmond et al. 2009; but see Knight & Temple 1986b) studies support the prediction of an increase in parental nest defence with offspring age.

The value of a clutch or brood to parents may also depend on the date of clutch initiation (Barash 1975; Weatherhead 1979; Curio et al. 1984; Montgomerie & Weatherhead 1988). For birds breeding in temperate zones, offspring-recruitment probabilities usually decline as the breeding season progresses (Harris et al. 1994; Moreno 1998; Shutler et al. 2006). If so, then late broods, characterised by low survival and recruitment prospects, are less valuable for parents and should be defended less intensively than early broods (Curio et al. 1984; Wallin 1987; Montgomerie & Weatherhead 1988; Redondo 1989). On the other hand, if females are capable of replacing a lost clutch following a failed breeding attempt, the reneesting potential will decline through a breeding season reaching a minimum when the opportunity to reneest in that breeding season is zero. Based on this assumption, the reneesting potential hypothesis (Barash 1975; Weatherhead 1979) predicts that a bird with low reneesting potential (i.e. late breeder) should defend more than a bird with high reneesting potential (i.e. early breeder) because the value of a

brood to the parents is directly proportional to the cost of replacing it (Dawkins & Carlisle 1976; Boucher 1977). Thus, while the offspring-survival prospects hypothesis predicts a decrease in nest defence with laying date, the reneesting potential hypothesis predicts an increase. Unfortunately, both offspring-survival prospects and reneesting potential usually decline through the breeding season in most bird species, precluding the appropriate evaluation of these hypotheses. This problem can be solved, however, by evaluating the offspring-survival prospects hypothesis in species with limited or no reneesting potential (e.g. Viñuela et al. 1995; Côté 2000).

Beyond the value of the brood, intensity of nest defence may also depend on the sex of the defending parent. In species showing sexual size dimorphism, intensity of nest defence may differ according to sex because larger birds are able to perform a stronger or more efficient defence, or because the vulnerability or risk of injuries are lower for the larger sex (Montgomerie & Weatherhead 1988; Kis et al. 2000; Tryjanowski & Goławski 2004).

Most studies testing nest defence hypotheses derived from parental investment theory have been carried out in passerines (Weatherhead 1979, 1989; Greig-Smith 1980; Knight & Temple 1986a,b; Curio & Regelmann 1987; Redmond et al. 2009) and raptors (Wallin 1987; Wiklund 1990; Galeotti et al. 2000; Kontiainen et al. 2009), with studies conducted on seabirds being comparatively scarce (Viñuela et al. 1995; Amat et al. 1996; Côté 2000; Kazama et al. 2010).

The Imperial Shag *Phalacrocorax atriceps* is a colonial ground-nesting seabird showing sexual size dimorphism with males being larger (~18%) than females (Svagelj & Quintana 2007). Both parents play an active role in nest defence, incubation, brood care and chick feeding duties throughout the breeding cycle (Svagelj 2009; Quintana et al. 2011; Svagelj & Quintana 2011a,b). This bird usually lays three-egg clutches with an incubation time of ~29 d, while chick-rearing period lasts for more than 2 mo (Svagelj & Quintana 2011a,b). Imperial Shags raise a single brood per year and exhibit a very limited reneesting potential with <1% of pairs attempting to breed twice in a season, always as a consequence of early breeding failures in their first attempt (Svagelj & Quintana 2011a). The number of days elapsed between the completion of the first and last clutches in the colony is usually ~6 wk (Svagelj & Quintana 2011a). Svagelj & Quintana (2011a) also showed that breeding success of Imperial Shags markedly decreases with laying date. In that study, probability

of breeding failure for late breeders was ten times higher than that for early breeders (Svagelj & Quintana 2011a). In addition, preliminary analysis of data based on mark–recapture of ringed birds suggests that survival probability of Imperial Shag fledglings also decreases with laying date (W. S. Svagelj & F. Quintana, unpubl. data). The system studied here therefore appears particularly appropriate for examining the offspring-survival prospects hypothesis in a seabird with a strong seasonal decline in offspring survival and very limited reneesting potential.

Using a stuffed model of a Kelp Gull *Larus dominicanus*, a recognised predator of eggs and chicks of seabirds (Quintana & Yorio 1998), we evaluated the influence of the number of offspring in the nest, offspring age, laying date and parent sex on the intensity of nest defence of the Imperial Shag. We predicted that the intensity of nest defence would increase with offspring number and age. Because breeding success and offspring-recruitment probabilities decrease as the breeding season progresses, we predicted a decrease in nest-defence intensity with laying date. Based on the sexual size dimorphism of the species, we also predicted that males, the larger sex, would have higher nest-defence intensity than females. In addition, we also evaluated whether the intensity of nest defence was correlated within pairs, predicting a within-pair positive relationship between male and female nest defence. Finally, we evaluated whether nest-defence intensity of both members of the pair was related with incubation and breeding success. Our predictions were that a positive relationship should exist between the intensity of nest defence and both incubation and breeding success.

Methods

This study was conducted from October to December 2008 at Punta León (43°05'S, 64°30'W), Chubut, Argentina. Punta León is a mixed-species seabird colony where Imperial Shags reproduce jointly with Kelp Gulls and other seabird species (see Yorio et al. 1994). At Punta León, the Kelp Gull has been reported to depredate eggs and chicks of the Imperial Shag, hunting almost exclusively from the ground by walking up to peripheral nests located at the edge of the colony (Quintana & Yorio 1998). Although Kelp Gulls may not represent a serious threat of life for breeding adults of the Imperial Shag, a higher investment in nest defence would be beneficial for breeding adults because Kelp Gulls are usual predators of egg and chicks of this species, and a positive

relationship between nest defence and offspring survival is expected.

Data were collected from 60 Imperial Shag peripheral nests. We checked nests every 1–3 d from the start of laying until completion of clutches. We also checked nests to establish the number of eggs completing the incubation period. During the chick-rearing period, we visited nests every 3–5 d to determine the fate of chicks. Chicks were considered to have fledged if they reached 30 d of age. To elicit Imperial Shag nest defence behaviour, we simulated a predation attempt by introducing a Kelp Gull model in close proximity to the shag nests. The gull dummy, attached to the end of a 4 m pole, appeared life-like and remained in good condition over the course of the study. Trials lasted five seconds and began when the dummy reached the nest ring. We recorded trials using a Sony CCD-TR700 (Sony Corporation, Tokyo, Japan) video camera recorder and scored defensive behaviour from these recordings. In all trials, W. S. Svagelj presented the gull dummy, while M. M. Trivellini recorded the shag response using the video camera.

In exploratory tests of our gull dummy, we identified pecks (i.e. individual pecks towards the dummy head and neck) and shakes (i.e. the defender grabs the dummy head with the bill and shakes it vigorously) as the two most frequent defensive behaviours. In consequence, we devised a scoring method that integrated these behaviours. Our index of nest-defence intensity [hereafter, nest-defence intensity (NDI)] was based on the number of pecks and shakes received by the dummy during a period of five seconds and calculated using the formula: $NDI = N^{\circ} \text{ pecks} + N^{\circ} \text{ shakes}$.

Experimental Design

To exclude the possible effect of a positive reinforcement in parental defence because of repeated tests in the same individuals (see Knight & Temple 1986a,b), each individual was tested only once. To test the effects of offspring number, offspring age, laying date and parent sex on NDI, we implemented a partly nested design with two crossed between-blocks factors and one within-blocks factor (see Quinn & Keough 2002; Logan 2010). Offspring age [three levels: early incubation (ca. 12 d of incubation), late incubation (ca. 26 d of incubation) and early chick rearing (chicks of ca. 6 d old)] and laying date (two levels: early and late breeders, representing the 1st and 3rd percentiles in laying date distribution, respectively) were the between-blocks

factors (i.e. a 3×2 factorial design) with 10 nests assigned to each combination of offspring age and laying date. The gull dummy was exposed one time to each parent for each nest, so parent sex (two levels: male and female) was the within-blocks factor. Nests were assigned to treatment groups maintaining equal median laying dates across treatments within laying-date levels and equal median offspring age across treatments within offspring-age levels (W. S. Svagej & F. Quintana, unpubl. data).

Statistical Analysis

To test the effects of offspring number, offspring age, laying date and parent sex on NDI, we employed generalised linear mixed models (Crawley 2007; Zuur et al. 2009; Logan 2010) with Poisson error distribution and log link function. Nest identity ($n = 60$) was included as a random effect. Offspring age, laying date and parent sex were included as categorical factors, while offspring number (i.e. number of eggs or chicks in the nest at the time of the trial) was included as a continuous variable.

We also evaluated the correlation in NDI between paired males and females and the relationship between NDI of pair members with incubation and breeding success. Because an individual's NDI score might be affected by offspring number, offspring age and trial date, we derived an adjusted NDI score [i.e. unbiased nest defence score, unaffected by brood value or trial date; hereafter, adjusted nest-defence intensity (ANDI)] using the residuals from a generalised linear model of NDI (error distribution = Poisson, link function = log) after removing possible confounding effects of the aforementioned variables. We ran a separate analysis for each sex, so residuals were normally distributed for each sex. To evaluate the relationship in ANDI between paired males and females, we used a Pearson's correlation test. To test the effects of ANDI scores of males and females and laying date – the explanatory variables – on incubation success (i.e. number of eggs completing the incubation period from eggs laid), we employed generalised linear models with binomial family distribution and logit link function (Crawley 2007). We also used generalised linear models (family distribution = Poisson, link function = log) to test the effects of explanatory variables on breeding success (i.e. number of chicks fledged per nest).

Models were evaluated with information-theoretic procedures (Burnham & Anderson 2002). We considered models with all possible combinations of predictor variables. This resulted in 16 candidate models

for the analysis of variation in NDI and eight models for incubation and breeding success analyses. Akaike's information criterion corrected for small sample size (AIC_c) was calculated for each model (Burnham & Anderson 2002). Model comparisons were made with ΔAIC_c , which is the difference between the lowest AIC_c value (i.e. best of suitable models) and AIC_c from all other models. The AIC_c weight of a model (w_i) signifies the relative likelihood that the specific model is the best of the suite of all models. We evaluated the support for predictor variables summing w_i across all models that contained the parameter being considered (parameter likelihood; Burnham & Anderson 2002). Parameter estimates were calculated using model-averaged parameter estimates based on w_i from all candidate models. To supplement parameter-likelihood evidence of important effects, we calculated 95% confidence interval limits (CL) of parameter estimates. Because models on incubation success exhibited overdispersion ($\hat{c} = 1.52$), we adjusted standard errors and used QAIC_c for model selection (Burnham & Anderson 2002). Statistical analyses were carried out using R software, Version 2.13.1 (R Development Core Team 2011). Values are reported as $\bar{x} \pm SE$ except where noted. All tests were two-tailed, and differences were considered significant at $p < 0.05$.

Results

All adult Imperial Shags responded aggressively to the gull dummy, with an average NDI of 13.6 (SD = 6.1, range 2–35; $n = 120$). The best model explaining the variation in NDI included offspring number, offspring age and parent sex as explanatory variables ($w_i = 0.66$; Table 1). NDI increased with offspring number and also differed between offspring-age categories (Table 2). NDI during chick rearing was higher than that at early and late incubation, while no differences were found between incubation stages (Table 2 and Fig. 1). Laying date was not related to NDI variation (early breeders: 14.1 ± 0.8 , $n = 60$; late breeders: 13.2 ± 0.8 , $n = 60$; Table 2). Also, NDI exhibited by males was higher than for females (males: 14.9 ± 0.8 , $n = 60$; females: 12.7 ± 0.7 , $n = 60$; Table 2).

Levels of adjusted nest-defence intensity (ANDI) of males and females within pairs were positively correlated ($r = 0.295$, $r^2 = 0.087$, $t_{58} = 2.4$, $p = 0.022$, $n = 60$; Fig. 2).

The best model explaining the variation in incubation success included laying date and male and female ANDI as explanatory variables ($w_i = 0.28$),

Table 1: Summary of model-selection results for models explaining variation in nest defence intensity (NDI) of the Imperial Shag in relation to offspring number (OFN), offspring age (AGE), laying date (LAY) and parent sex (SEX). *k* is the number of estimated parameters. See methods for details. Models are listed in decreasing order of importance

Candidate models	<i>k</i>	AIC _c	ΔAIC _c	<i>w_i</i>
OFN AGE SEX	6	214.9	0.0	0.662
OFN AGE LAY SEX	7	216.8	1.9	0.248
AGE SEX	5	219.8	4.9	0.057
AGE LAY SEX	6	221.3	6.4	0.027
OFN AGE	5	225.2	10.3	0.004
OFN AGE LAY	6	227.1	12.2	0.001
AGE	4	230.1	15.2	0.000
OFN SEX	4	230.8	15.9	0.000
SEX	3	231.1	16.2	0.000
AGE LAY	5	231.6	16.7	0.000
LAY SEX	4	232.6	17.7	0.000
OFN LAY SEX	5	232.6	17.7	0.000
OFN	3	241.2	26.3	0.000
Null model	2	241.5	26.6	0.000
OFN LAY	4	243.0	28.1	0.000
LAY	3	243.0	28.1	0.000

Table 2: Parameter likelihoods, estimates (± SE) and 95% confidence interval limits (CL) for explanatory variables describing variation in nest defence intensity (NDI). Explanatory variables with CL excluding zero are in bold. See methods for details

Explanatory variable	Parameter likelihood	Parameter estimate ± SE	CL	
			Lower	Upper
Intercept		1.84 ± 0.24	1.39	2.30
Offspring number	0.92	0.19 ± 0.07	0.05	0.33
Offspring age (late incubation) ^a	1.00	0.15 ± 0.10	-0.05	0.35
Offspring age (chick rearing) ^a	1.00	0.48 ± 0.10	0.28	0.67
Laying date (late season) ^b	0.28	-0.05 ± 0.08	-0.21	0.11
Sex (males) ^c	0.99	0.18 ± 0.05	0.08	0.27

^aRelative variable to value of offspring age (early incubation).

^bRelative variable to value of laying date (early season).

^cRelative variable to value of sex (female).

although there was considerable model uncertainty (Table 3a). This model explained 18% of variation in incubation success. Early breeders had higher incubation success than late breeders (Table 4a). Neither male nor female ANDI was related to incubation success, as both CL encompassed zero (Table 4a).

Average breeding success was 0.83 fledglings per nest (SD = 0.78, n = 60), ranging from 0 to 2 fledglings. The best model explaining the variation in

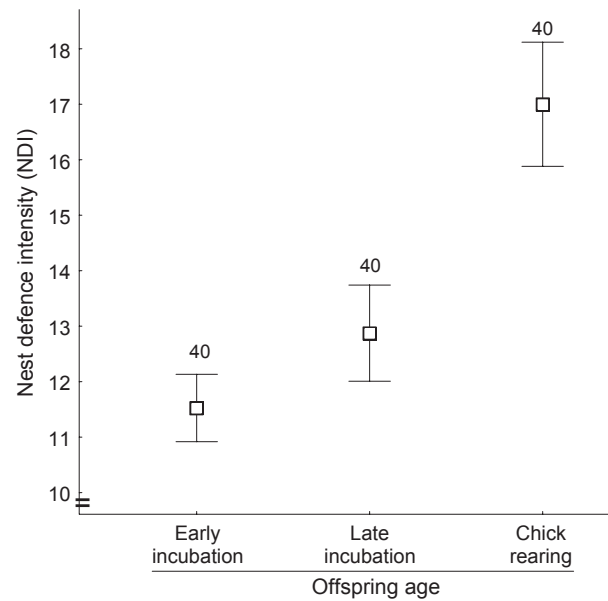


Fig. 1: $\bar{x} \pm SE$ of nest-defence intensity (NDI) of Imperial Shags according to offspring age [early incubation (ca. 12 d of incubation), late incubation (ca. 26 d of incubation) and early chick rearing (chicks of ca. 6 d old)]. Numbers indicate sample size.

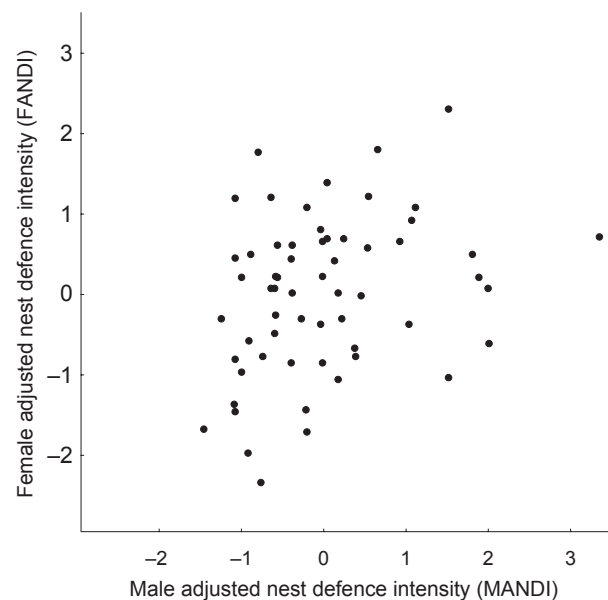


Fig. 2: Adjusted nest-defence intensity by the male (MANDI) and female (FANDI) of each pair of Imperial Shags (n = 60). Adjusted nest-defence intensity scores were the residuals derived from a generalised linear model of nest-defence intensity (NDI) after removing the effects of offspring number, offspring age and trial date. See methods for details.

Table 3: Summary of model-selection results for models explaining variation in (a) incubation success and (b) breeding success of the Imperial Shag in relation to laying date (LAY) and adjusted nest defence intensity of males (MANDI) and females (FANDI). *k* is the number of estimated parameters. See methods for details. Models are listed in decreasing order of importance

Response variable	Candidate models	<i>k</i>	QAIC _c	ΔQAIC _c	<i>w_i</i>
(a)					
Incubation success	LAY MANDI FANDI	4	76.1	0.0	0.275
	LAY FANDI	3	76.2	0.1	0.262
	LAY MANDI	3	76.5	0.4	0.217
	MANDI FANDI	3	78.6	2.5	0.078
	MANDI	2	78.9	2.8	0.067
	LAY	2	79.2	3.1	0.057
	FANDI	2	80.1	4.0	0.036
	Null model	1	83.2	7.1	0.008
(b)					
Breeding success	LAY	2	122.6	0.0	0.563
	LAY FANDI	3	124.7	2.1	0.190
	LAY MANDI	3	124.8	2.2	0.186
	LAY MANDI FANDI	4	127.0	4.4	0.060
	Null model	1	139.7	17.1	0.000
	MANDI	2	141.3	18.7	0.000
	FANDI	2	141.8	19.2	0.000
	MANDI FANDI	3	143.5	20.9	0.000

breeding success included laying date as an explanatory variable (*w_i* = 0.56; Table 3b); this model accounted for 34% of variation. Early breeders produced four times more fledglings than late breeders (1.33 ± 0.11, *n* = 30 and 0.33 ± 0.16, *n* = 30, for early and late breeders, respectively; Table 4b). Neither male nor female ANDI was related to variation in breeding success (Table 4b).

Discussion

Offspring Number

Parental investment theory predicts that parents should defend a large brood more vigorously than a smaller one because the former contributes a higher proportion of genes to its lifetime reproductive output (Trivers 1972; Dawkins & Carlisle 1976; Maynard Smith 1977). Our findings agree with theory in this respect as nest defence by Imperial Shags was positively related to the number of offspring in the nest. Previous studies in which brood size was left unmanipulated (as in this study) have provided variable results in relation to the brood size hypothesis; while some studies support the predicted increase in nest defence with brood size (Knight & Temple 1986a; Wallin 1987; Kontiainen et al. 2009), others do not (Viñuela et al. 1995; Tryjanowski & Goławski 2004; Redmond et al. 2009). Because a positive relationship between the level of nest defence and clutch or brood size may merely reflect the quality of the parents (see Curio & Regelmann 1987), clutch or brood size manipulation experiments have been carried out to exclude an effect of parental quality in nest defence (Wiklund 1990; Amat et al. 1996; but see Kazama et al. 2010). A similar approach could be applied to our system in future studies to confirm a causal relationship between offspring number and nest defence.

Offspring Age

In most species studied so far, offspring age seems to be the main factor explaining variation in the level

Response variable	Explanatory variable	Parameter likelihood	Parameter estimate ± SE	CL	
				Lower	Upper
(a)					
Incubation success	Intercept		1.56 ± 0.41	0.75	2.37
	Laying date (late season) ^a	0.81	-1.05 ± 0.48	-2.00	-0.10
	Male ANDI	0.65	0.55 ± 0.32	-0.08	1.18
	Female ANDI	0.64	0.47 ± 0.26	-0.05	0.98
(b)					
Breeding success	Intercept		0.29 ± 0.16	-0.03	0.61
	Laying date (late season) ^a	1.00	-1.39 ± 0.36	-2.10	-0.68
	Male ANDI	0.25	0.01 ± 0.14	-0.27	0.29
	Female ANDI	0.25	0.03 ± 0.17	-0.29	0.36

Table 4: Parameter likelihoods, estimates ± SE, and 95% confidence interval limits (CL) for explanatory variables describing variation in (a) incubation success and (b) breeding success of the Imperial Shag. Explanatory variables with CL excluding zero are in bold. See methods for details

ANDI, adjusted nest-defence intensity.

^arelative variable to value of laying date (early season).

of parental nest defence (see Montgomerie & Weatherhead 1988). Our study provides additional support for parental investment theory as nest-defence intensity of Imperial Shags increased with offspring age. While nest-defence intensity during chick rearing was clearly higher than during early and late incubation (55% and 32% higher, respectively), there were no differences between incubation stages. The lack of differences within the incubation period could be because the reproductive value of the offspring increases only marginally at the early stages of the breeding cycle (i.e. egg laying and incubation; see Montgomerie & Weatherhead 1988). Rate of change in reproductive value is likely greatest at later stages of the breeding cycle (i.e. nestling and fledgling period), with the increase in reproductive value accelerating with increasing offspring age (Montgomerie & Weatherhead 1988; Redondo 1989).

Laying Date and Offspring-Survival Prospects

Curio et al. (1984) proposed a model of nest defence that takes into account a variation in offspring-survival prospects, predicting that the intensity of parental defence would be directly proportional to the expected survival of the offspring at stake. Thus, if offspring survival decreases when breeding begins later in the season, early breeders should defend their offspring more than later ones. This hypothesis was supported by studies in raptors and passerines (Wallin 1987; Wiklund 1990; Kontiainen et al. 2009; Redmond et al. 2009), but support from any seabirds is lacking.

The Imperial Shag is a seabird species with marked seasonal decline in offspring survival and very limited re-nesting potential (Svagelj & Quintana 2011a). Despite that, we failed to find an association between parental defence and laying date, even though the counteractive confounding effect of re-nesting potential can be ignored in our study system (see introduction). Although it is unclear why Imperial Shags similarly defended early and late broods, another study (Côté 2000) in a seabird species with strong seasonal decline in chick survival (King Penguin *Aptenodytes patagonicus*) also failed to find differences in nest defence according to laying date. It must be noted that parental investment in current offspring may depend not only on its reproductive value but also on the residual reproductive value of the parents (Stearns 1992). As Imperial Shags are long-lived birds, the possible effect of parental age on investment in nest defence remains to be evaluated.

Parent Sex and Intrapair Correlation

The intensity of nest defence may be sex-dependent if costs and benefits differ between sexes (Montgomerie & Weatherhead 1988; Redondo 1989). A larger and heavier bird not only should be able to engage in stronger nest defence for the same relative costs (e.g. risk of injury) as those for a smaller or weaker bird, but it should also be more effective in deterring predators than a smaller bird (Andersson & Norberg 1981; Montgomerie & Weatherhead 1988). In sexually dimorphic species, the larger sex often defends nests more vigorously than the smaller (Galeotti et al. 2000; Kis et al. 2000; but see Tryjanowski & Goławski 2004). Thus, higher nest defence exhibited by males of the Imperial Shag may be a consequence of their bigger structural body size in relation to females.

For monogamous species with biparental care and no sex-specific parental roles, a positively correlated response is expected because mates defend the same nest, and hence, the same brood value (Breitwisch 1988; Weatherhead 1989). Moreover, even for the same brood value, if the intensity of parental nest defence is positively related to predator deterrence, assortative mating with regard to nest defence is expected (Breitwisch 1988; Weatherhead 1989). Here, after statistically controlling for factors affecting brood value, we found a positive within-pair correlation in nest defence by Imperial Shag mates. In this species, both sexes share nest defence throughout the breeding cycle. Also, Imperial Shags at Punta León exhibit a marked sexual difference in daily activity rhythms during the egg laying, incubation and early chick-rearing phases, with females feeding in the morning and males in the afternoon, the latter leaving the nest only when their mates return. Thus, from the start of egg laying until chicks reach 15–20 d of age, at least one member of the pair is always at the nest caring for and protecting the nest contents while their mate is foraging. Therefore, adult Imperial Shags would benefit by mating assortatively with regard to nest defence. Alternatively, a positive correlation in nest defence may also arise if one parent adjusts its defence according to defence behaviour of its mate (Weatherhead 1989). Unfortunately, the separating of these hypotheses is beyond the scope of the current study.

Nest Defence, Incubation Success and Breeding Success

Several studies have shown that parents who defend their nests more vigorously suffer lower nest preda-

tion than less vigorous defenders (Andersson et al. 1980; Knight & Temple 1986a; Tryjanowski & Goławski 2004; but see Redmond et al. 2009). In this study, however, neither male nor female nest defence levels were related to incubation or breeding success variation. These results suggest that other factors, such as laying date or parental quality and age, play a much larger role in determining the outcome and productivity of an Imperial Shag nesting attempt (Svagelj & Quintana 2011a).

In summary, our study provides partial support for parental investment theory. While parental nest defence of Imperial Shags increased with brood value according to offspring number and offspring age, parental defence was not related to laying date, a factor strongly affecting offspring survival in this species.

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