



Behavioral Ecology (2019), XX(XX), 1–7. doi:10.1093/beheco/arz049

Original Article

Sharing the burden: on the division of parental care and vocalizations during incubation

Marwa M. Kavelaars,^{a,b,✉} Luc Lens,^b and Wendt Müller^a^aBehavioural Ecology and Ecophysiology Research Group (BECO), University of Antwerp, Universiteitsplein 1, 2610 Antwerp, Belgium and ^bTerrestrial Ecology Unit (TEREC), Ghent University, K.L. Ledeganckstraat 35, 9000 Ghent, Belgium

Received 9 May 2018; revised 12 February 2019; editorial decision 13 March 2019; accepted 20 March 2019.

In species with biparental care, individuals only have to pay the costs for their own parental investment, whereas the contribution of their partner comes for free. Each parent hence benefits if its partner works harder, creating an evolutionary conflict of interest. How parents resolve this conflict and how they achieve the optimal division of parental tasks often remains elusive. In this study, we investigated whether lesser black-backed gulls (*Larus fuscus*) divide parental care during incubation equally and whether this correlates with the extent of vocalizations between pair-members during incubation. We then investigated whether pairs showing more evenly distributed incubation behavior had a higher reproductive success. To this end, we recorded incubation behavior and vocalizations for 24-h time periods. Subsequently, we experimentally increased or decreased brood sizes in order to manipulate parental effort, and followed offspring development from hatching till fledging. Although incubation bouts were, on average, slightly longer in females, patterns varied strongly between pairs, ranging from primarily female incubation over equal sex contributions to male-biased incubation. Pairs contributing more equally to incubation vocalized more during nest relief and had a higher reproductive output when brood sizes were experimentally increased. Thus, vocalizations and a more equal division of parental care during incubation may facilitate higher levels of care during the nestling period, as suggested by a greater reproductive success when facing high brood demand, or they indicate pair quality.

Key words: equality, gulls, negotiation, parental care, parental investment, sexual conflict.

INTRODUCTION

Parental care increases offspring survival, but comes at a cost for the parents (Trivers 1972; Curio 1988). Given that resources are limited, individuals of iteroparous species should therefore optimize their reproductive output by balancing the investment in current offspring against self-maintenance, in order to secure future reproductive opportunities (Trivers 1972). An individual's parental provisioning behavior, and therewith the amount and type of parental care to be provided, depends among others on the individual's intrinsic condition (e.g., Newton and Rothery 1997) as well as on sex-specific task specialization during reproduction such as nest-defense, egg-laying, or incubation behavior (e.g., Iserbyt et al. 2014). Furthermore, the environment, comprising temporal and spatial fluctuations in biotic and abiotic factors such as food availability and weather conditions, has a significant effect on parental

care (e.g., Kosztolányi et al. 2009). In biparental species, the trade-off between current and future benefits is, however, additionally confounded by an evolutionary conflict of interest over parental investment (Trivers 1972; Houston et al. 2005), because both parents pay the costs of care individually, but share the overall benefits. It is therefore in both parents' interest that their partner provides more care than they do themselves (Trivers 1972; Lessells and McNamara 2012). The resolution of this conflict may require some form of behavioral negotiation over parental investment (Lessells and McNamara 2012). Selection in fact favors reproductive strategies that promote cooperation between partners, and theoretical models predict that more successful cooperation can be reached via behavioral negotiation over parental investment (McNamara et al. 1999).

To this end, individuals may have to monitor their partner's investment when determining the amount of care they will provide. Individuals might, for example, only invest more if their partner has done so before, and through reciprocity, pairs may reach more efficient levels of parental investment (Gächter 2007; Johnstone

Address correspondence to M.M. Kavelaars. E-mail: marwa.kavelaars@uantwerpen.be.

et al. 2014). But, even though pair-members can estimate the contribution of the partner in an indirect way, via the condition of the offspring or their begging behavior (e.g., Hinde 2006), the opportunities for parents to monitor each other's contribution directly are relatively sparse during the chick-rearing period. Parents spend—depending on the species—little time at the nest due to high rates of nestling provisioning, and even more so when they have to travel far distances to reach their foraging grounds. It may require explicit behavioral strategies, such as turn-taking or synchronization of foraging patterns and feeding visits, in order to monitor each other's contribution and to coordinate parental investment (Johnstone et al. 2014; Mariette and Griffith 2015). Ultimately, coordination of foraging behavior between partners is indeed found to correlate with reproductive success (Mariette and Griffith 2012, 2015). Parental coordination can increase over time in species with long-term pair bonds (Coulson 1966; Van De Pol et al. 2006), and via social interactions, such as vocal communication (Hall 2000; Elie et al. 2010) and repeated social displays (Emery et al. 2007). These pair displays likely contribute to pair bond maintenance (Elie et al. 2010) and may additionally function as a way to directly coordinate the levels of care between the partners (Wachtmeister 2001).

In birds, most studies investigated whether individuals adjust their levels of care to that of their partner when parents were providing food for their nestlings (Velando and Alonso-Alvarez 2003; Hinde 2006; Bijleveld and Mullers 2009). However, often both sexes already incubate the eggs, which requires a substantial investment of time and energy, so the same conflict arises and cooperation during incubation may again only be reached via behavioral negotiation. Furthermore, adjusting to each other's levels of investment may be even more important during the early stage of reproduction (Bulla et al. 2017), as a given level of parental cooperation may be predictive for parental care strategies at later stages (Morris 1987). The nest typically cannot be left unattended during this phase neither because discontinuity of breeding could lead to embryonic developmental problems (Olson et al. 2006) or to predation (Conway and Martin 2000). Therefore, when both sexes share incubation, the parents have to take turns incubating the clutch continuously. They consequently encounter each other at nest relief, which is often accompanied by vocalizations. Boucaud et al. (2016) showed that accelerated vocal duets at nest relief resulted in a faster return of the foraging parent, who determines the length of its partner's incubation bout. Hence, parents could signal their condition to their partner (Boucaud et al. 2016), but may also communicate about their contribution to parental care (Wachtmeister 2001).

Nest relief is thus a valuable moment for the exchange of information, making the incubation period well-suited to study parental cooperation and the consequences of the division of care, because the task performed by both partners is the same, facilitating a quantification of their contributions. The necessity to negotiate about parental investment is expected to be higher at the beginning of reproduction when information about the amount of effort the partner is going to invest may be more limited (Lessells and McNamara 2012). The division of parental care established during incubation is likely to be maintained during chick rearing (Morris 1987). Finally, incubation of the eggs is a mutually exclusive event, meaning that parents cannot change their contribution independently of each other without increasing the risk of reproductive failure (see above).

In this experiment, we studied the within-pair equality in a common parental care task, incubation behavior, in lesser black-backed

gulls (*Larus fuscus*), a seabird species with long-term pair bonds, and how that correlates with reproductive success. To this end, we investigated how pairs divided their amount of care during incubation and assessed if equality in parental care during incubation co-varied with the levels of vocalizations during nest relief. Such vocalizations may either indicate aspects of pair quality or they may facilitate parental cooperation. We then studied whether pairs that had a more equal share in incubation were more successful in raising offspring. Offspring demand was additionally altered via brood size manipulation in order to test whether the consequences of more evenly distributed contributions to incubation increase when conditions to raise offspring are more challenging. We expected that the most successful pairs communicate more during the incubation period. Furthermore, we hypothesized that pairs showing a high level of equality in care during incubation will achieve the highest reproductive output, here measured in terms of offspring growth. We expected the effect of equality in incubation behavior to be most evident in nests with an increased brood size because parental cooperation becomes particularly relevant when dealing with high-offspring demand.

MATERIAL AND METHODS

Field work

Lesser black-backed gull nests were monitored in 3 consecutive breeding seasons (from mid-April until mid-July in 2015–2017) in the colony of Vlissingen-Oost, the Netherlands (51°27'N, 3°42'E). Nests were checked every other day (laying interval is about 48 h) and the laying date of each egg was indicated using a nontoxic marker. Both parents of the nests were color-ringed for individual identification. Standard morphometric measurements were taken which allowed us to distinguish males from females in all pairs (Ingolfsson 1969). Cameras (420TVL, with infrared function) were placed at the nest at 50–100 cm distance to film on day 7, 14, and/or 21 after clutch completion. Cameras were removed after approximately 24 h of continuous recordings, creating each time 27 ± 3.5 h of video recordings (2015: $N = 22$; 2016: $N = 20$; 2017: $N = 26$). During video recordings, all pairs were incubating their own eggs. The modal clutch size in our species is 3 eggs, and all experimental clutches were complete during the video recordings.

Pairs were then randomly divided into low-demand nests (1 chick, $N = 32$ nests) and high-demand nests (3 chicks, $N = 36$ nests; natural brood size in study population is 1.7 at fledging). At the moment of hatching, the complete clutch of the focal pairs was, to this end, replaced by, respectively, 1 or 3 pipping eggs that were taken from surrounding nests with similar laying—and thus—hatching dates. When we cross-fostered 3 eggs into 1 experimental nest, these eggs came from 3 different nests, but had identical hatching dates. We only used first or second laid eggs for our experimental nests, as the third egg is often of lower quality. Through this cross-foster design, we manipulated brood sizes while keeping egg hatching synchronized at the nest level. Thereby, we avoided the occurrence of any runt chicks in the nests, as natural lesser black-backed gull clutches hatch asynchronously, and hatching order-related mortality is common (Kim et al. 2010). By increasing the chance of survival of all 3 chicks in the enlarged nests for a longer period of time, we aimed to increase parental effort. The eggs of the experimental nests were placed in the nests of the donor pairs or in nests with similar laying dates that were partly depredated. These nests were not followed prior to or after cross-fostering.

Chicken wire enclosures were built around each nest (ca. 2×2 m in size, and 0.3 m high) to ensure that the chicks stayed close to the nest for the entire developmental period. PVC tubes were added to provide shelter, since chicks could not hide in the surroundings. On the day of hatching, chicks were individually marked with colored tape and down feathers were sampled for molecular sexing. Offspring development (body mass) was measured every 2–3 days until fledging (day 30) and chick mortality was recorded during each visit.

Behavioral analysis

Behavioral analyses of the videos were performed using *The Observer XT* software (Noldus, The Netherlands). The parent that was incubating the eggs was identified by its color-rings, and the duration of the incubation bout was scored. Additionally, we quantified all vocalizations during nest relief, that is, when both parents were present at the nest. All types of calls that have typically been associated with pair formation and pair bond maintenance were scored, consisting among others of long calls, choking, and mew calls (for an extensive description of the displays, see Tinbergen 1960). The duration of the vocalizations was measured from the beginning of each call until its end, and these values were summed up for each pair (see Supplementary Material for a video fragment of vocalizations during nest relief).

We were restrained from filming all nests twice ($N = 20$) or 3 times ($N = 8$) due to a shortage of camera equipment. However, the division of incubation is found to be consistent across the whole incubation period (Morris 1987; Stenhouse et al. 2004; Bartlett et al. 2005). We, therefore, also included the nests that we only managed to observe once ($N = 40$).

Statistical analyses

All statistical analyses were conducted in R (R Development Core Team 2017).

A binomial generalized linear mixed-effect model was fitted to investigate whether females and males differed in the proportion of share in total incubation time. The model was carried out with the *lme4* package (Bates et al. 2015), with proportion of incubation time modeled as response variable, sex modeled as fixed factor, and nest ID modeled as random effect. To compare the average length of incubation bouts between the sexes, a Student's *t*-test was used. Pairs were subsequently categorized as “equal” or “unequal” based on the division of time spent incubating. A ratio of $50 \pm 10\%$ was defined as *equal*, and any pair with one of the parents spending more than 60% of the time incubating was assigned as *unequal*.

A Wilcoxon rank-sum test was then carried out to compare calling behavior between equal and unequal pairs.

The consequences of equality in incubation behavior on offspring quality were assessed via linear mixed effects models using the *lme4* package (Bates et al. 2015). As environmental conditions varied across years, and offspring development in lesser black-backed gulls differs between the sexes (Griffiths 1992), we standardized offspring growth between years and sexes by creating a Body Condition Index (BCI) for each year and both sexes separately. For each chick, we first calculated the deviation from the average group body mass at each measurement by subtracting the chick's body mass at age t by the average body mass of all chicks at age t . The deviation at age t was subsequently divided by the average body mass at age t , to correct for a higher deviation at an older age (see Stienen et al. 2015 for a comparable approach),

$$\text{BCI} = \frac{\text{body mass at age } t - \text{average body mass at age } t}{\text{average body mass at age } t}$$

In the linear mixed effects model, BCI was explained by year (2015, 2016, 2017), brood size (1, 3), and equality (equal, unequal), as well as all possible 2-way and 3-way interactions. Data points are not independent as chicks were measured multiple times, and within the same nest, they receive care from the same parents. This was accounted for by adding random effects on the individual chick level as well as the nest level (chick ID nested in nest ID). Linear mixed models were carried out testing the effects of year and equality for nests with 1 and 3 chicks separately.

RESULTS

Behavioral analyses

Incubation share varied strongly among pairs (Figure 1). Many pairs divided incubation within the range that we defined as equal ($50 \pm 10\%$ contribution by each individual), whereas others divided their time incubating less equally [$N(\text{eq}) = 28$, $N(\text{uneq}) = 40$]. In pairs with unequal incubation patterns it was either the male or the female who incubated more (Figure 1).

The proportion of time spent incubating the clutch was female-biased (females = 0.54, males = 0.46, $z = -2.718$, $P = 0.007$). Female and male incubation bouts lasted on average 4 h and 47 min (± 8.9 min), and 4 h and 10 min (± 8.0 min), respectively ($t_{190} = 3.068$, $P = 0.003$).

Equal pairs spent more time calling than unequal pairs [Mann-Whitney $U = 515$, $N(\text{eq}) = 28$, $N(\text{uneq}) = 40$, $P = 0.024$; Figure 2].

Developmental consequences

BCI was best explained by brood size ($F_{1,88.54} = 50.948$, $P \leq 0.001$) and the interaction between year and brood size ($F_{2,89.47} = 6.612$, $P = 0.002$; Table 1). To disentangle interaction effects, the data set was successively split by brood size. Further analysis with a separation of the data into brood sizes showed a year effect on BCI in nests with 1 chick ($F_{2,27.480} = 5.352$, $P = 0.011$; Figure 3), but no effect of equality ($F_{1,27.51} = 0.198$, $P = 0.660$). In contrast, in the nests with 3 chicks, only equality had a significant effect on BCI,

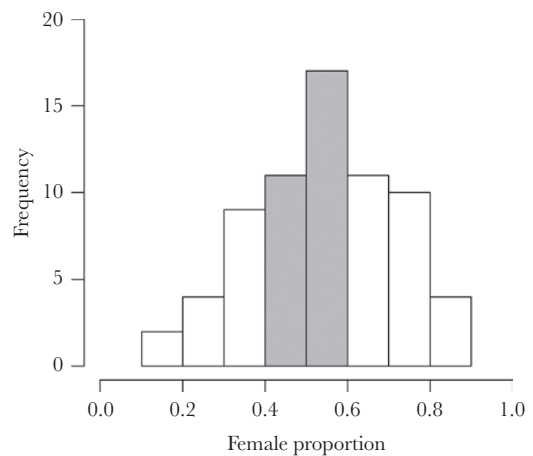


Figure 1 Frequency distribution of the proportion of female incubation behavior in 24-h video observations. Gray bars show the area that is allocated as equal division of incubation between males and females (0.5 ± 0.1).

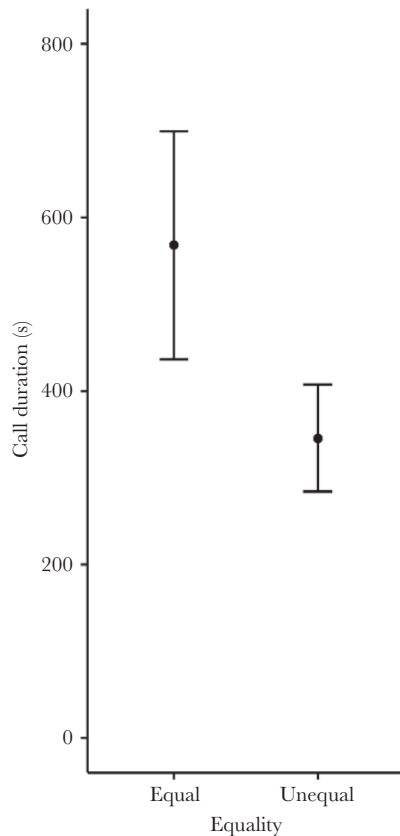


Figure 2

Total amount of time (average \pm s.e.) pairs spent calling in seconds during 24-h of continuous video observations, for both equal ($N = 28$) and unequal ($N = 40$) lesser black-backed gull pairs.

with equal pairs having offspring with higher BCI ($F_{1,33.20} = 4.376$, $P = 0.044$).

DISCUSSION

We investigated how equal lesser black-backed gull parents contribute to a common task during reproduction, incubation behavior, and whether equality in parental care during the early reproductive phase is indicative of reproductive success. Incubation patterns varied strongly between pairs, with some pairs contributing equally to incubation, whereas in other pairs either the male or the female individual was found to incubate more than its partner. An equal contribution to incubation, which co-varied with a higher amount of vocalizations during nest relief, resulted in a higher offspring quality when brood demand was elevated.

Division of labor between the sexes

In many species, males and females specialize in certain parental behaviors, including incubation behavior (e.g., Iserbyt et al. 2017), resulting in a sex-specific efficiency. In this context, it is argued that the parent incubating most efficiently should contribute more to incubation (Parker et al. 2014). In our study, females incubated, on average, slightly more than males, spending 54% of the time on the nest, opposed to 46% in males. This difference is likely due to the longer incubation bouts in females. The results of our study are in accordance with the findings in other gull species, showing that incubation is on average rather equally distributed between sexes,

Table 1

Linear mixed effects model testing the effects of equality (equal or unequal contribution to incubation), year (2015, 2016, 2017), brood size (1 or 3 chicks, experimental brood size manipulation), and their interactions on body condition index of offspring (BCI)

	Source of variation	Full models		
		d.f.	<i>F</i>	<i>P</i>
Combined 1 + 3 chicks	Equality	1	2.515	0.116
	Brood size	1	49.219	<0.001
	Year	2	1.004	0.371
	Equality \times year	1	0.743	0.391
	Equality \times brood size	2	0.202	0.818
	Brood size \times year	2	6.276	0.003
	Equality \times brood size \times year	2	0.231	0.794
1 Chick	Equality	1	0.198	0.660
	Year	2	5.352	0.011
	Equality \times year	2	0.092	0.913
3 Chicks	Equality	1	4.376	0.044
	Year	2	2.004	0.151
	Equality \times year	2	0.451	0.641

Data are split for the brood sizes in order to facilitate the interpretation of the observed interaction effect. Chick ID nested in nest ID was included as a random effect.

fluctuating around the 50% level. The female–male ratio was, for example, 50.3% versus 49.7% in herring gulls (*Larus argentatus*; Drent 1967), 53.5% versus 46.7% in black-headed gulls (*Larus ridibundus*; Ytreberg 1956), and 46% versus 54% in black-legged kittiwakes (*Rissa tridactyla*; Coulson and Wooller 1984). Among pairs, incubation was found to be both male- and female-biased, which renders it unlikely that there is a consistent, sex-specific specialization during incubation. Males may still contribute more to nest defense (Pierotti 1981), but this was not evident in our data. In our video observations, males were rarely seen fighting. However, it has to be taken into account that the cameras covered a limited range of territory, whereas competition is likely most severe along territory borders outside of that range. Courtship feeding, the act in which a male provides the female with regurgitated food, could be another male-specific parental task during incubation. However, the amount of courtship feeding decreases after egg laying (Salzer and Larkin 1990) and has only been observed occasionally on the videos (personal observation). The absence of a strong task specialization in our study species during incubation suggests that an equal contribution should be the optimal division of parental effort within pairs.

Among-individual variation in incubation behavior may not only relate to the efficiency of incubation. An alternative explanation for variation in the duration of incubation bouts could relate to the gulls' foraging behavior. The foraging partner is the one who determines the duration of its partner's incubation bout (Niebuhr and McFarland 1983), as the nest cannot be left unattended. Lesser black-backed gulls are known to specialize in acquiring a specific type of food and depending on the foraging specialization some individuals spent more time foraging. Indeed, a recent study found that male lesser black-backed gulls foraged more often offshore, whereas females predominantly foraged on land or near-shore (Camphuysen et al. 2015). Trip duration was consequently longer in males than in females. If the relieving bird is the one to

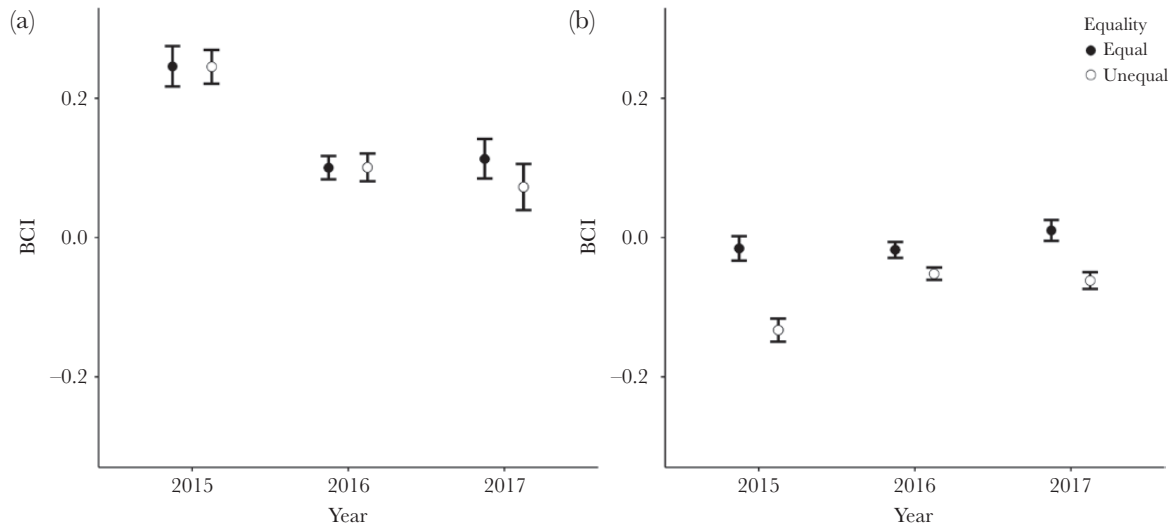


Figure 3

Body condition index (BCI) (average \pm s.e.) for chicks of (a) small 1-chick broods (reduced brood demand) and (b) large 3-chick broods (increased brood demand) for parents that incubated equally (black circles) or unequally (white circles), separated for 3 years of study.

determine when nest relief takes place (Niebuhr and McFarland 1983), its foraging behavior might influence the duration of the foraging trip and thereby the duration of the incubation bout of its partner. However, as pointed out above, we did not find significant sex differences in incubation behavior, as would be expected if foraging behavior would play a significant role, given the males' longer foraging bouts (Camphuysen et al. 2015). Further investigation using GPS tracking systems would nevertheless be necessary to directly relate foraging strategies to incubation behavior, to allow a better understanding of both within- and between-pair variation in parental investment in incubation.

Vocalizations during nest relief

When individuals returned to the nest to relieve their partner, this was often accompanied by ritualized, social interactions, such as choking or mew calls between the mates, and sometimes a session of calling was followed by the partners carrying out nest maintenance together. Yet, on other occasions, nest relief happened without any vocalizations or social interactions, and the relieved individual left the territory immediately after the return of the partner.

Pairs that vocalized to a greater extent divided their incubation duties more equally, whereas pairs with a skewed distribution of care were found to vocalize less (Figure 2). Nest relief ceremonies are a widespread phenomenon in biparental species and are typically interpreted in the context of communication (reviewed in Wachtmeister 2001). As other behavioral displays, they may contribute to pair bond maintenance (Elie et al. 2010), which is particularly important during the early stage of reproduction. The behavior of the birds during nest relief may thus reflect aspects of pair compatibility or pair bond duration, both are known to affect reproductive success (Coulson 1966; Niebuhr and McFarland 1983; Van De Pol et al. 2006; Ihle et al. 2015).

Individuals could potentially also signal their physiological status to their partner in order to divide the parental effort (Boucaud et al. 2016; Takahashi et al. 2017). Therewith communicating to their partner whether they are staying or leaving when meeting each other at the nest (Boucaud et al. 2017). Communication at this moment could thus function as a way to directly coordinate the

levels of care between the partners (Wachtmeister 2001), which is crucial for an optimal division of parental care between partners.

The adaptive significance of equality in incubation

Pairs that shared the incubation task more equally were more successful in raising offspring. However, this effect only became apparent when parents raised nests with 3 chicks that hatched synchronously. Equality in incubation behavior did not have significant effects on offspring development in pairs raising a single chick. This suggests that pairs that shared their care equally during incubation were more successful in adapting to enhanced brood demand, as our brood size manipulation in fact tested whether parents were able to adapt to and to accommodate the increased offspring demand (Mariette and Griffith 2015).

Our results fit with the concept of reciprocity (Taborsky et al. 2016), which implies that a parent invests into care when the partner invests as well, which may lead to more efficient, higher overall levels of investment (Johnstone et al. 2014). That is to say, individuals are more likely to contribute to a shared investment when others are also willing to do so (Gächter 2007). This, however, assumes in our study that the division of care that is established during incubation is maintained throughout the breeding period as was found in herring gulls (Morris 1987). Equal contributions to care are also thought to become more likely with increasing pair-bond duration, which then again has positive effects on reproductive success (Van De Pol et al. 2006). Unfortunately, we have as of yet not enough long-term data to test this.

As pointed out above, the division of care within pairs might be of increased importance in harsher situations, as reflected in the effect of equality on body condition in enlarged broods. We also observed significant differences in offspring conditions across years, likely related to the occurrence and timing of heat waves in 2 years of our study, which combined with the resulting drought can lead to a low food availability and thus negatively affects breeding success in seabirds (Oswald et al. 2008; Oswald and Arnold 2012). However, year differences in chick body condition were only present in nests with low offspring demand and did not vary with

the parental equality in incubation behavior. When parents were challenged by enlarged broods, body condition of the chicks was consistently lower than in the single chick broods independent of the environmental conditions, indicating that our experimental manipulation substantially increased parental effort. Taken together, environmental factors as well as behavioral aspects—here the division of care during incubation—are thus important factors determining reproductive success but may act on different scales, thereby giving an indication of the complexity of parental care strategies.

CONCLUSIONS

In gulls, parents cannot change their share in incubation independently of each other so that nest relief is an important moment of contact during incubation. Our data suggest that this moment was used for communication, and parents that vocalized more at the moment of nest relief contributed more equally to incubation. Equal pairs better accommodated experimentally increased brood demand when compared with unequal pairs, as reflected in higher offspring quality. Likely because equal pairs were better in increasing their rate of provisioning when their brood was experimentally enlarged. However, further research on the levels of investment during the chick-rearing phase is necessary in order to investigate the interplay between parental investment during incubation and offspring provisioning. Furthermore, studying whether vocal communication plays a causal role for the coordination of parental tasks, how equality relates to pair compatibility, as well as whether and how equality improves with increasing pair bond duration, likely represent fruitful avenues for future research.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

FUNDING

This work was supported by the Research Foundation Flanders (FWO id: 11ZI716N and G0E1614N).

AUTHOR CONTRIBUTIONS

M.M.K. collected and analyzed the data; M.M.K., L.L., and W.M. discussed the analytical approach and results; M.M.K. drafted the manuscript with support from L.L. and W.M.

We thank Nastazja Tylzanowski, Aurélie Dailledouze, Jorn Suijkerbuijk, and Sergio Delgado Acero for their support in the field, and we are grateful to Roland-Jan Buijs for all the ringing effort. We also thank Zeeland Seaports for their permission to access the port, and COVRA, EPZ, Pacorini, and Van Citters Beheer BV for access to their sites. Eric Stienen and Jan Baert provided valuable comments on an earlier version of this manuscript. We are also very grateful to 2 anonymous reviewers and handling editor Andrea Griffin for their useful comments. All procedures performed in this study have been approved by the ethical committee of the University of Antwerp (file number 2013-73) and the ethical committee of the University of Groningen (file number 6986/6986A).

Conflict of interest: The authors declare that they have no conflict of interest.

Data accessibility: Analyses reported in this article can be reproduced using the data provided by Kavelaars et al. (2019).

Handling Editor: Andrea Griffin

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