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Sex allocation from an owl perspective: clutch order could determine brood sex to reduce sibling aggression in the Eagle Owl *Bubo bubo*

Vincenzo Penteriani, Maria M. Delgado, Juan M. Pérez-García, Francisco Botella, Santiago García, José A. Sanchez Zapata, Mario L. Ortega, José E. Martínez, José F. Calvo, Joaquín Ortego, Giulia Penteriani, Mario Melletti, Igor Krugersberg & Olga M. Talavera

V. Penteriani, M.M. Delgado, M. Melletti & O.M. Talavera, Department of Conservation Biology, Estación Biológica de Doñana, C.S.I.C., c/ Americo Vespucio s/n, 41092 Seville, Spain. E-mail penteriani@ebd.csic.es
V. Penteriani, Finnish Museum of Natural History, P.O. Box 18, FI-00014 University of Helsinki, Finland
M.M. Delgado, Laboratory of Ecological and Evolutionary Dynamics, Department of Biological and Environmental Sciences, FI-00014 University of Helsinki, Finland
J.M. Pérez-García, F. Botella, S. García & J.A. Sanchez Zapata, Área de Ecología, Dpto. Biología Aplicada, Universidad Miguel Hernández, Avda. de la Universidad, s/n. Edif. Altabix, 03202 Elche (Alicante), Spain
M.L. Ortega, J.E. Martínez & J.F. Calvo, Departamento de Ecología e Hidrología, Universidad de Murcia, Campus de Espinardo, 30100 Murcia, Spain
J. Ortego, Grupo de Investigación de la Biodiversidad Genética y Cultural, Instituto de Investigación en Recursos Cinegéticos (CSIC-UCLM-JCCM), Ronda de Toledo s/n, E-13005 Ciudad Real, Spain
G. Penteriani & I. Krugersberg, Urb. Golf, 42109 Las Pajanosas, Spain

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Hatching asynchrony in altricial bird species occurs if incubation starts before clutch completion. It determines differential within-brood growth, which may result in a competitive and developmental hierarchy among siblings. As a consequence, asymmetric sibling competition frequently results in post-hatching mortality of the last-hatched offspring. Because nestling hierarchy is not necessarily adaptive, species that are able to raise large broods should have evolved mechanisms to reduce within-brood mortality due to sibling competition. One mechanism to reduce offspring mortality could be to favour the occurrence of the larger sex among late-laid chicks. We explored this possibility by studying the sex allocation of 349 Eagle Owl (*Bubo bubo*) chicks from 137 broods, as a function of clutch size and order. In broods of four chicks, parents seemed to invest in the less energetically expensive sex (male) at the third position, and females (the larger sex) as the last, and therefore smallest, chick in the brood. This strategy should reduce asymmetric sibling competition: the relative position of chicks of each sex within the brood is likely to be crucial for maximizing the success of clutches.

1. Introduction

Hatching asynchrony in altricial birds (see Magrath 1990 & Stenning 1996) is the serial production of offspring that occurs when the incubation of asynchronously laid eggs starts before clutch completion (Clark & Wilson 1981). Hatching asynchrony has several, mutually non-exclusive consequences. These include (a) within-brood differential growth, particularly manifested in large broods when the time interval in egg-laying is more than one day; (b) a competitive hierarchy among nestling broodmates, and (c) asymmetric sibling competition, frequently resulting in post-hatching mortality of the last-hatched offspring (Magrath 1990). Siblicidal brood reduction (Mock 1985, 1994, Gonzalez-Voyer *et al.* 2007) can occur directly, usually through wounding, and indirectly, e.g., through forced starvation or expulsion from the nest, even when parental care and trophic resources are not limiting (Pijanowski 1992). The phenomenon occurs mainly in species that have weaponry such as claws and sharp beaks, including birds of prey (e.g., Bortolotti 1986a,b). However, in owls siblicide is rare even though they generally produce large broods with a time interval between the laying of eggs exceeding one day (Mikkola 1983, Voous 1988).

The nestling hierarchy, determined by asynchronous hatching, could be a by-product of the commencement of incubation prior to clutch completion. Hierarchy may be a strategy for (a) better adjusting for variation in resource availability, i.e., brood survival may be considered optimal under circumstances where food resources are unpredictable; (b) decreasing embryonic mortality due to adverse weather; and/or (c) reducing the growth of pathogens at mild temperatures through increasing egg temperature (Stenning 1996, Beissinger & Stoleson 1997, Sockman 2008). Species able to raise large broods should accordingly have evolved mechanisms to reduce within-brood mortality caused by sibling aggression. Evidence for intra-brood competition is abundant, including the negative effect of increasing brood size on growth, size and survival of offspring (Parker *et al.* 2002, Royle *et al.* 2004). One way to reduce offspring mortality caused by siblicide is to favour the production of the larger sex among late-laid chicks; see Oddie (1998) and Komdeur & Pen (2002) for a general overview of adaptive sex allocation in birds.

To gain a deeper understanding on factors determining sex allocation in long-lived species showing reverse sexual size dimorphism and large clutches (here, four chicks), we explored two mutually non-exclusive hypotheses, that both have the potential to explain sex allocation as a function of clutch order. We thus evaluated sex allocation in Eagle Owl (*Bubo bubo*) broods as a function of clutch order, by putting forward the following hypotheses:

Hypothesis 1 (the energetic cost hypothesis): the costs of feeding and caring for young are assumed to vary among reproductive phases (e.g., Dijkstra *et al.* 1990, Golet *et al.* 1998, Parker *et al.* 2002). Following Fisher's (1930) hypothesis, as parental expenditure on progeny of both sexes is equal, chicks of the energetically less expensive sex should more frequently be produced later in large clutches. Males are smaller than females in the Eagle Owl and thus presumably represent the energetically less expensive sex, as observed in some birds of prey and owls (e.g., Bednarz & Hayden 1991, Appleby *et al.* 1997, Krijgsveld *et al.* 1998; but see Mcdonald *et al.* 2005 and references therein), and hence require fewer resources (Anderson *et al.* 1993). We thus predicted that male chicks would be more common than female chicks as the 3rd and 4th, as opposed to 1st and 2nd, offspring to reduce the energetic costs of brood-rearing. The main assumption was that only the offspring size matters: we thus only considered the effect of size. Sex-specific aggressive behaviour among siblings and the overall costs and benefits of rearing different sexes could not be determined using the present data. For example, males might be more aggressive than females and consequently obtain more food as chicks. Moreover, producing large daughters gives a disproportionate advantage in terms of having grandchildren; hence the net investment may be lower than that for raising sons of similar quality.

Hypothesis 2 (the reduced sibling aggression hypothesis): if body size is a poor indicator of potential parental costs and/or the larger sex does not significantly increase the biological costs on parents (Mcdonald *et al.* 2005), sex allocation within a brood could partly result from a reduction of conflicts among nestlings (e.g., Bortolotti 1986a, b, Magrath *et al.* 2003, Carranza 2004, Uller 2006). In such instances physical strength would be important in shaping the competitive relationship among siblings (Parker *et al.* 2002). In this case, two scenarios can be envisaged. (1) Due to the species' sexual dimorphism, sibling aggression or competition for food is likely to be extremely strong between the first- and the last-hatched chicks. Consequently, more females would be expected among third- and fourth-hatched chicks if the first-hatched is a female. In fact, a female that hatches first in a brood will rapidly become substantially larger and heavier than a male that hatches the fourth (Penteriani *et al.* 2005), consequently increasing the risk of mortality of the smallest young. (2) Because the Eagle Owl is slightly size-dimorphic (Delgado & Penteriani 2004), the sex (and consequently the size) of the first-hatched chick may not be important in determining sex allocation and, due to the competition among the first- and last-hatched chicks, more females should still be expected among the third- and fourth-hatched chicks, irrespective of the sex of the first-hatched chick.

2. Material and methods

2.1. Study area and species

The study was conducted during five breeding seasons in 2003–2007 in an area consisting of several geographical subunits in southern Spain: (1) the Sierra Norte of Seville (the Sierra Morena massif, southwest Spain), a hilly area ranging 60–200 m a.s.l. (Penteriani *et al.* 2005); and (2) three neighbouring hilly areas in the Murcia and Alicante regions (south-eastern Spain) including a coastal massif in the Murcia region (0–629 m a.s.l.); the Sierras of Columbares, Altaona and Escalona (40–646 m a.s.l.); and the Cordillera Sur, a hilly area ranging from 50–400 m a.s.l.. These subunits share Mediterranean climate, general landscape attributes (small hills with open forest, shrubs and patches of agricultural land) and high availability of rabbits (*Oryctolagus cuniculus*), the main prey of the Eagle Owl in Mediterranean habitats (Delibes & Hiraldo 1979). Breeding density of Eagle Owls is ca. 40 territories per 100 km^2 over the whole study area.

The Eagle Owl is a long-lived species (>15 yrs in the field and >60 yrs in captivity; Penteriani 1996), distributed throughout the Palaearctic region, and the largest owl in the world (body mass ca. 1.5–4 kg). It is sexually plumage-monomorphic but females are on average larger than males. In the Mediterranean region, egg-laying typically starts in mid-December and, while clutch size can vary from 1 to 5 eggs, extremes are rare. The eggs are generally laid at 2-day intervals, egg-laying begins before clutch completion, and as a result hatching is asynchronous (Mikkola 1983). Intriguingly, the Eagle Owl is the largest avian predator able to produce large clutches and to successfully fledge the whole brood. Siblicide is rare (V. Penteriani & M.M. Delgado, unpubl. data), in contrast with other owl species (Mikkola 1983, Houston *et al.* 1998, Moser 2002). The Eagle Owl is particularly appropriate for testing our hypotheses, as it has many traits that facilitate the evolution of aggressive competition among siblings (Gonzalez-Voyer *et al.* 2007). These include (a) direct feeding predominating throughout the nestling period (i.e., the food passes directly from the adult's to the chick's beak). Selection favours sibling aggression in species in which dominant chicks can monopolize the food the parents bring to the nest. (b) effective weaponry (larger nestlings are able to injure smaller brood mates). (c) nest-site topography that reduces chances for escaping, such as cliffs, caves and large trees. (d) differences in age and size of brood mates due to hatching asynchrony. (e) food items are often large and infrequent, clustered in bouts or meals. As aggression is more costly than begging or fighting for food, larger food items are a significant reward for the aggressor. (f) long nestling period (at least approx. 35 days), which favours aggressive interactions among brood mates and increases the possibility that cohabitation will coincide with periods of food shortage.

2.2. Sex ratio in the study population

As the first step to testing the two study hypotheses, we estimated the size frequency and the proportion of males (hereafter sex ratio for convenience) for broods from SW and SE Spain, and for both areas combined. Sex ratio was the number of male chicks over all chicks. To evaluate if Eagle Owl parents are able to control the sex ratio of their chicks, for the same areas we (a) assessed the similarity of the observed sex ratio with an expected sex ratio of 50:50 using the binomial test (Hardy 2002) and (b) tested the fit of the observed sex ratio with a binomial distribution (i.e., the distribution predicted by evolutionary theory; Hardy 2002). This involved a comparison of the deviance of the null model to the c^2 distribution of the observed data with degrees of freedom equal to the null degrees of freedom. Positive results of one or both of these tests should indicate non-random variation in the sex ratio distribution.

Determination of the hatching order of nestlings by monitoring egg-laying and hatching sequence appears difficult because of the risk of nest abandonment due to nest disturbance (V. Penteriani & M.M. Delgado, unpubl. data). Moreover, if nests are observed when owlets are 30–40 days old, determination of the hatching order may be complicated due to sexual size dimorphism. To overcome these limitations, we examined the studied broods when their offspring were less than 1 month old, at which age the effect of hatching asynchrony predominates over that of sexual dimorphism (see Penteriani *et al.* 2005). We obtained blood from the owlets, extracted the DNA, and used these data to sex the chicks through molecular procedures (Griffiths *et al.* 1998).

2.3. Evaluating within-brood order of different sexes

We used Bayesian techniques (e.g., McCarthy 2007) to test whether within-brood sex is at least partly due to the number and sequence of eggs laid, which constituted the background required to explore our study hypotheses. Bayes' theorem is a method for calculating conditional probabilities. Bayes' theorem combines (1) prior probabilities (the estimates of the degree of confidence in each hypothesis before the data are seen), and (2) the probabilities of the data (the probability that the data would be observed if each hypothesis was true). The combination produces posterior probability estimates, which represent the degree of belief in each hypothesis under consideration. That is,

$$P(A|B) = \frac{P(B|A)P(A)}{P(B)} \tag{1}$$

where $P(A)$ and $P(B)$ are the prior probabilities of events A and B, respectively. Prior probabilities of one event do not take into account any information about other events; $P(A|B)$ is the conditional probability of A, given the event B. This is a posterior probability because the probability of A depends on the probability of B. In this case we say that $P(A|B)$, the probability that A is true given that B is true, is the posterior probability of A. Thus $P(A|B)$ represents the probability assigned to A after taking into account the new piece of evidence, B; and $P(B|A)$ is the conditional probability of B, given the event A.

Conditional probability represents the probability that one proposition is true provided that another proposition is true. It is not a primitive notion, and can be defined in terms of absolute probabilities, e.g., $P(A|B) = P(A \text{ and } B) / P(B)$ (i.e., the probability that A and B are both true divided by the probability that B is true).

It should be noted that different sample sizes can occur within broods of the same size when the sex of one of the chicks is unknown. For example, within a three-chick brood the sex allocation of the third chick can be calculated with respect to the first if the sex of the second chick is unknown, but sex probabilities between the first and the third chicks with respect to the second cannot be calculated.

We report the probabilities of the entire set of possible sex combinations within a brood for descriptive reasons, but we included only broods of three or four chicks in our analyses. The temporal gap between the first and the last chick (approximately 6 days for 1st and 4th chick) enables an easier detection of the presence of any given sex-distribution pattern.

2.4. Statistical analyses

Subsequent to the Bayesian analysis, and to confirm the possible non-random variation in the sex-ratio distribution, we used the SAS GLIMMIX (version 8.2) to test for (a) the sex of the third chick as a function of both the brood size and the sex of the first chick (both variables considered as fixed

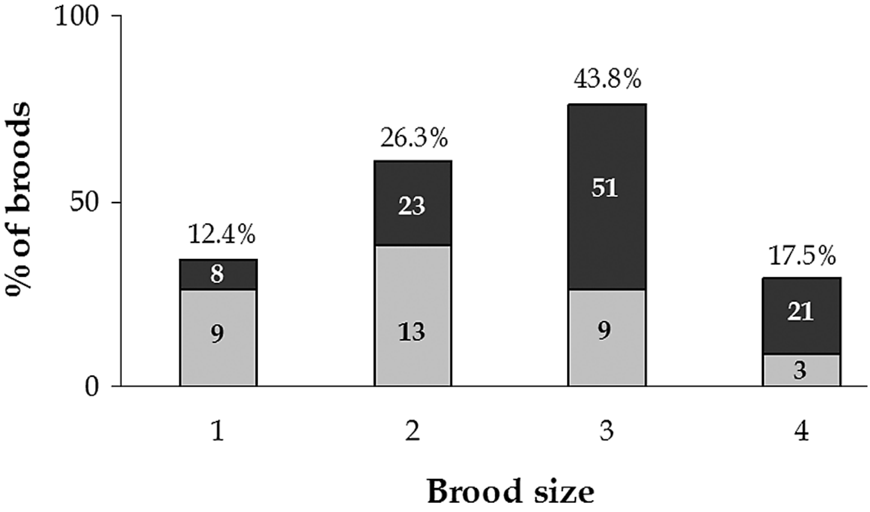


Fig. 1. Brood-size frequencies in 137 Eagle Owl broods, sampled during 2003–2007 in south-western (grey bars) and south-eastern Spain (black bars). Numbers on columns denote sample sizes (*N*). Values with percent symbols show pooled frequencies from both study areas.

factors), as well as their interaction; and (b) the sex of the fourth chick as a function of the sex of the other chicks (fixed factors), and their interactions. In both analyses the nest was considered a random factor. As outlined above, all of the studied nests were in similar geographical areas. Consequently we did not consider "geographical subunit" as an additional factor in the models. All statistical analyses were performed with SAS and SPSS software.

3. Results

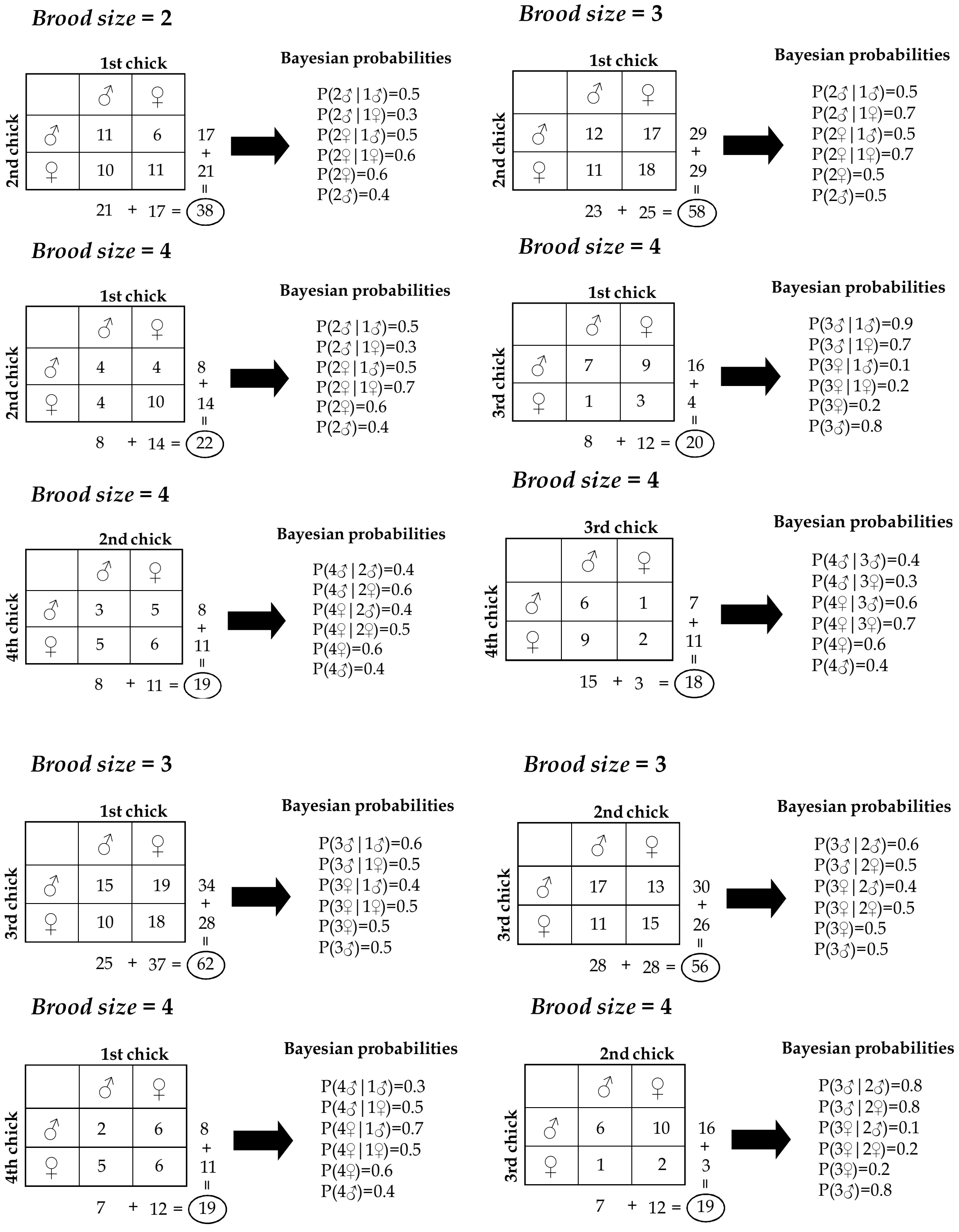
3.1. Sex ratio of owlets, and clutch sizes

We determined the sex of 349 eagle owl chicks from 137 broods (SW Spain = 34 and SE Spain = 103 broods) during the five study years. The sex ratio of owlets in both regions was close to 0.5 (SW Spain = 0.46, $P = 0.3$; SE Spain = 0.53, $P = 0.6$; binomial tests), corresponding to the general sex ratio of 0.48 ($P = 0.5$; binomial test). However, SW Spain ($\chi^2_{87} = 121.6$, $P < 0.0025$), SE Spain ($\chi^2_{260} = 369.4$; $P < 0.001$) and both samples combined ($\chi^2_{348} = 483.3$, $P < 0.001$) differed significantly from a binomial distribution, suggesting a parental control on sex allocation. The proportion of different brood sizes were, respectively for SW and SE Spain, 26.5% and 7.8% (1 chick), 38.2% and 22.3% (2 chicks), 26.5% and 49.5% (3 chicks), and 8.8% and 20.4% (4 chicks) (Fig. 1). These percentages were not significantly different from modal clutch sizes that were 2 for SW and 3 for SE Spain (SW Spain: $\chi^2_3 = 0.5$, $P < 0.8$; SE Spain: $\chi^2_3 = 0.0$, $P = 1$; both samples combined: $\chi^2_3 = 0.0$, $P = 1$).

3.2. Probabilities for a given sex within the brood

Bayesian probabilities generally showed that, for clutch sizes of four eggs, (1) there was a high probability (78.95%) that the 3rd chick was a male (partially supporting the energetic cost hypothesis), and (2) the 4th chick was slightly more frequently a female (57.89%; Fig. 2). The latter probability was not apparently affected by the hatching of a female as the 1st chick, the probability that the 4th chick was a female being only of 33.33% (reduction of sibling aggression hypothesis, scenario 1).

The GLIMMIX analyses supported the results obtained by the Bayesian estimation of probabilities for the energetic cost hypothesis for the sex of the 3rd chick (brood size: $F = 5.34$, $P = 0.02$; sex of the 1st chick: $F = 0.97$, $P = 0.34$; brood size × sex of the 1st chick: $F = 0.25$, $P = 0.62$). Although the probability that the 4th chick was a female was approximately 60% in Eagle Owl broods, the generalized linear mixed model did not indicate significant relationships between the sex of the 4th chick and the sex of the other chicks, including their interactions.



Brood size = 2

1st chick

2nd chick	♂	♀	
♂	11	6	17
♀	10	11	21
	21	17	38

Bayesian probabilities

P(2♂ | 1♂)=0.5
P(2♂ | 1♀)=0.3
P(2♀ | 1♂)=0.5
P(2♀ | 1♀)=0.6
P(2♀)=0.6
P(2♂)=0.4

Brood size = 3

1st chick

2nd chick	♂	♀	
♂	12	17	29
♀	11	18	29
	23	25	58

Bayesian probabilities

P(2♂ | 1♂)=0.5
P(2♂ | 1♀)=0.7
P(2♀ | 1♂)=0.5
P(2♀ | 1♀)=0.7
P(2♀)=0.5
P(2♂)=0.5

Brood size = 4

1st chick

2nd chick	♂	♀	
♂	4	4	8
♀	4	10	14
	8	14	22

Bayesian probabilities

P(2♂ | 1♂)=0.5
P(2♂ | 1♀)=0.3
P(2♀ | 1♂)=0.5
P(2♀ | 1♀)=0.7
P(2♀)=0.6
P(2♂)=0.4

Brood size = 4

1st chick

3rd chick	♂	♀	
♂	7	9	16
♀	1	3	4
	8	12	20

Bayesian probabilities

P(3♂ | 1♂)=0.9
P(3♂ | 1♀)=0.7
P(3♀ | 1♂)=0.1
P(3♀ | 1♀)=0.2
P(3♀)=0.2
P(3♂)=0.8

Brood size = 4

2nd chick

4th chick	♂	♀	
♂	3	5	8
♀	5	6	11
	8	11	19

Bayesian probabilities

P(4♂ | 2♂)=0.4
P(4♂ | 2♀)=0.6
P(4♀ | 2♂)=0.4
P(4♀ | 2♀)=0.5
P(4♀)=0.6
P(4♂)=0.4

Brood size = 4

3rd chick

4th chick	♂	♀	
♂	6	1	7
♀	9	2	11
	15	3	18

Bayesian probabilities

P(4♂ | 3♂)=0.4
P(4♂ | 3♀)=0.3
P(4♀ | 3♂)=0.6
P(4♀ | 3♀)=0.7
P(4♀)=0.6
P(4♂)=0.4

Brood size = 3

1st chick

3rd chick	♂	♀	
♂	15	19	34
♀	10	18	28
	25	37	62

Bayesian probabilities

P(3♂ | 1♂)=0.6
P(3♂ | 1♀)=0.5
P(3♀ | 1♂)=0.4
P(3♀ | 1♀)=0.5
P(3♀)=0.5
P(3♂)=0.5

Brood size = 3

2nd chick

3rd chick	♂	♀	
♂	17	13	30
♀	11	15	26
	28	28	56

Bayesian probabilities

P(3♂ | 2♂)=0.6
P(3♂ | 2♀)=0.5
P(3♀ | 2♂)=0.4
P(3♀ | 2♀)=0.5
P(3♀)=0.5
P(3♂)=0.5

Brood size = 4

1st chick

4th chick	♂	♀	
♂	2	6	8
♀	5	6	11
	7	12	19

Bayesian probabilities

P(4♂ | 1♂)=0.3
P(4♂ | 1♀)=0.5
P(4♀ | 1♂)=0.7
P(4♀ | 1♀)=0.5
P(4♀)=0.6
P(4♂)=0.4

Brood size = 4

2nd chick

3rd chick	♂	♀	
♂	6	10	16
♀	1	2	3
	7	12	19

Bayesian probabilities

P(3♂ | 2♂)=0.8
P(3♂ | 2♀)=0.8
P(3♀ | 2♂)=0.1
P(3♀ | 2♀)=0.2
P(3♀)=0.2
P(3♂)=0.8

Fig. 2. Schematic representation of the Bayesian probabilities of sex allocation in Eagle Owl broods (see text for details). Tables on the left show the number of offspring of a given sex with regard to the sex of the other chicks, for broods of two, three and four chicks. The total sample size for each table is circled: different samples within a brood of the same size occur because of the lack of information on the sex of some chicks in the same brood. Bayesian probabilities for both the absolute occurrence of a sex within a brood and the occurrence of a sex with respect to the other chicks of the same brood are shown on the right.

4. Discussion

The main pattern highlighted in the sex allocation of large broods of Eagle Owls could be considered a trade-off between the energetic cost hypothesis and the scenario 2 within the framework of the reduced sibling aggression hypothesis. In broods of four chicks, Eagle Owls seemed to invest in the less energetically costly sex as the 3rd hatchling (favouring the hatching of males). This could favour the production of female chicks (the larger sex) as the last (and smallest among the chicks in the nest) of the brood. This strategy has the potential to reduce sibling aggression. Our results are consistent with previous reports of within-brood sex composition, the maternal strategies for adjustment of broodmate sex being the result of selection to minimise the detrimental effects of sex-specific sibling interactions and the costs of investment in reproduction, to maximise the fecundity of breeders (e.g., Bortolotti 1986a,b, Bednarz & Hayden 1991, Wiebe & Bortolotti 1992, Legge *et al.* 2001, Badyaev *et al.* 2002, Carranza 2004, Royle *et al.* 2004, Režalová *et al.* 2005, Blanco *et al.* 2006, Uller 2006).

The patterns of sex allocation that we observed in Eagle Owls could be a means of resolving the apparent paradox represented by the contrasting effects of hatching asynchrony vs. sibling rivalry in those species that can raise large broods. If hatching asynchrony is adaptive (Szöllősi *et al.* 2007, Sockman 2008), but has the collateral effect of increasing brood-mate aggression and killing, a possible solution would be to commence incubation prior to clutch completion as a way of increasing egg viability (Arnold *et al.* 1987, Veiga 1992, Sockman 2008), and to adjust sex allocation within broods to favour the larger sex as the last hatchers (to eliminate or reduce sibling aggression). As the risk of siblicide mainly depends on the sex composition of the brood, difference in hatchling size may be an important factor involved in siblicide. However, the reasons for the effects of intra-brood sex ratio on siblicide are not well understood (Uller 2006), but even if the adjustment of sex ratio within broods appears important, the success of clutches may be determined by the relative position of each sex within the brood (see also Uller 2006). In the Eagle Owl, the sex composition that provides the highest number of surviving offspring (Karlin & Lessard 1983) could be the one that produces a female as the last chick in broods of four eggs in cases when the energetically less expensive male is the 3rd chick.

We only focused on hypotheses related to a specific aspect of within-brood sex allocation, and consequently we cannot exclude the role of other factors contributing to sex allocation. However, by studying the same populations at multiple areas over several years, we probably reduced potentially confounding effects of variability in environmental conditions affecting our populations (Parker *et al.* 2002, Sasvári & Nishiumi 2005, Desfor *et al.* 2007). There is a relationship between hatching order and sex allocation, with females being able to control the sex of chicks hatching from individual eggs in the laying sequence (Carranza 2004). Because post-hatching control is likely to be energetically more expensive and directly affects the lifetime reproductive success of individuals (Ležalová *et al.* 2005), pre-ovulation control mechanisms should be favoured in species able to produce large broods, in particular through manipulation of the sex of offspring in high ranking positions within the brood.

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Syntymäjärjestys saattaa määritellä poikasen sukupuolen ja tätä kautta vähentää sisarusten keskinäisiä aggressioita huuhkajalla

Pesäviipyisillä linnuilla kuoriutuminen on usein eriaikaista, kun haudonta alkaa jo ennen muninnan päättymistä. Kuoriutumisen eriaikaisuus määrittelee sisarusten kasvueroja, mikä edelleen voi johtaa sisarusten keskinäiseen kilpailuun ja hierarkkisuuteen. Tämän seurauksena epäsymmetrinen kilpailu sisarusten kesken johtaa usein viimeisinä kuoriutuneiden poikasten kuolemaan. Koska pesäpoikashierarkia ei välttämättä ole sopeuttavaa, suuria pesyeitä tuottavilla lajeilla voidaan olettaa kehittyvän mekanismeja sisaruskilpailun aiheuttamia poikaskuolemia vastaan.

Yksi tällainen mekanismi voi olla suurempikokoisen sukupuolen suosiminen viimeksi munituilla jälkeläisillä. Asiaa selvittääksemme tutkimme sukupuoliallokointia 349 huuhkajan (*Bubo bubo*) poikasella, jotka olivat peräisin 137 pesyeestä. Tarkastelimme erityisesti pesyekokoa ja kuoriutumisjärjestystä. Neljän poikasen pesyeissä emot näyttivät investoivan energeettisesti edullisempaan (koiras) sukupuoleen kolmanneksi kuoriutuneen poikasen kohdalla, mutta investoivan naaraisiin (aikuisina isompia) viimeisenä kuoriutuneiden (ja siksi pienempikokoisten) kohdalla. Tämä strategia voi vähentää sisaruskilpailua: eri sukupuolten kuoriutumisen ajoittuminen voi olla ratkaisevan tärkeää pesimämenestyksen kannalta.

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