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Fighting for fitness

Salomons, Henri Martijn

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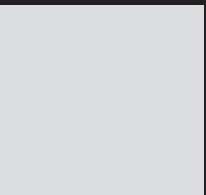
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Strong but variable associations between social dominance and clutch sex ratio in a semi-colonial corvid

H. Martijn Salomons
Cor Dijkstra
Simon Verhulst

Summary

We studied primary sex ratio of clutches in relation to social dominance for six years in a colony of free-living jackdaws, a small corvid. Social dominance was strongly associated with clutch sex ratio, with the difference in clutch sex ratio between the most and least dominant pairs being 30-40%. To our knowledge, this is the first demonstration of an association between social dominance and sex allocation in birds. However, the direction of this effect varied between years. Dominant jackdaws produced more sons during the first years of the study, but fewer sons during the last years. Offspring sex was not related to laying order within a clutch, and the effect of social dominance on sex ratio was similar on eggs laid first, middle or last. We investigated the effect of two factors (laying date and parental condition) that could have mediated the shift in the effect of social dominance on sex allocation in the course of the study. Laying date was positively associated with the proportion of males, but this effect was independent of social dominance. Maternal condition (residual mass over tarsus, egg volume) was related to social dominance, but not to clutch sex ratio. Paternal condition (residual mass over tarsus) was not related to clutch sex ratio. We discuss how spatial or temporal variation in effects of variables such as social dominance on sex allocation can contribute to our understanding of the evolution of sex allocation in species with complex life histories.

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Introduction

Sex allocation theory predicts that parents should bias resource allocation towards the sex that yields the highest net fitness benefits (Trivers & Willard 1973; Charnov 1982; Frank 1990). Parents can allocate resources differentially between sons and daughters in various ways. In birds, females may for instance vary the volume of their eggs, and thereby the available resources, depending on the sex of the embryo (Anderson et al. 1997; Magrath et al. 2003; Müller et al. 2005). Parents can also differentiate the amount (Nishiumi et al. 1996) or quality (Magrath et al. 2004) of food delivered to sons and daughters (Lessells et al. 1998). However, the most direct strategy to modify sex allocation is through adjustment of the primary sex ratio of offspring (Fisher 1930; Charnov 1982; Pike & Petrie 2003; Alonso-Alvarez 2006), and here we focus on the latter variant of sex allocation in free-living jackdaws *Corvus monedula*.

Evidence for biased sex allocation in birds has accumulated in recent years (see Pike & Petrie 2003; Alonso-Alvarez 2006 for reviews). Most of these studies focus on specific life history traits to explain observed differences in sex biased resource allocation. For instance in kestrels offspring sex ratio (% males) was negatively related to laying date of the clutch (Dijkstra et al. 1990b). Other studies showed biased sex allocation in relation to maternal condition (Nager et al. 1999; Pike 2005), paternal quality or attractiveness (Burley 1981; Svensson & Nilsson 1996; Pike & Petrie 2005b; Fawcett et al. 2007). In many species the fitness prospects of offspring decline with laying order, thus adjusting offspring sex would be particularly beneficial in the first eggs of a clutch. Indeed such laying order dependent biases in the level of sex ratio manipulation have been reported for many bird species (Weatherhead 1985; Dijkstra et al. 1990b; Albrecht 2000). Food availability has also been shown to affect sex allocation decisions in for

example the kakapo *Strigops habroptilus* (Clout et al. 2002) and the seychelles warbler *Acrocephalus sechellensis* (Komdeur 1996).

In social animals, groups are usually structured in the sense that when there is a conflict some individuals are consistently more successful at obtaining resources than others (Allee 1952; Drews 1993). Thus, if resource access or condition is important in determining optimal sex allocation, it is to be expected that social dominance is often associated with sex allocation. This hypothesis has been extensively studied in mammals (Clutton-Brock & Iason 1986; Brown & Silk 2002; Sheldon & West 2004), but has been little studied in birds. Moreover, to our best knowledge the avian studies that investigated this hypothesis found no support for dominance dependent sex allocation: domestic fowl, *Gallus gallus* (Leonard & Weatherhead 1996; Müller et al. 2002), peafowl, *Pavo cristatus* (Pike & Petrie 2005a) and black-capped chickadees, *Poecile atricapilla* (Ramsay & Ratcliffe 2003). However, in collared flycatchers *Ficedula albicollis* there is indirect evidence for an effect of social dominance on sex allocation, because males with a large forehead patch are more successful in competition over nest boxes (Qvarnström 1997), and females mated to such males produce more sons (Ellegren et al. 1996). Similarly, in great tits *Parus major* the size of the breast stripe is correlated with social dominance (Lemel & Wallin 1993), and there was a positive trend in the relation between breast stripe size and clutch sex ratio (Kolliker et al. 1999). Furthermore, paternal tarsus length, another correlate of resource holding potential in this species (Garnett 1981), was also related to brood sex ratio variation in the same species (Kolliker et al. 1999; Yamaguchi et al. 2004). However, in house sparrows *Passer domesticus* there is an effect of badge size on social dominance (Møller 1987), but no relation was found between male badge size and the number of sons and daughters produced (Husby et al. 2006).

Social dominance plays a major role in the life of jackdaws (Lorenz 1931). Being dominant

provides primary access to nesting opportunities and food (Röell 1978) and also affects breeding success (Henderson & Hart 1995; Verhulst & Salomons 2004). Jackdaws are moderately sexually size dimorphic at fledging, with males being 5–10% larger than females (Salomons et al, unpublished results), indicating that higher costs are involved in producing male offspring. When one sex is more costly to produce than the other this indicates that the relationship between parental investment and fitness benefits differs between sons and daughters. The details of these relationships have to be known to predict the optimal sex allocation in response to variation in resource access (Leimar 1996; Komdeur & Pen 2002), but the moderate sexual size dimorphism in itself increases the likelihood that the optimal sex allocation depends on parental resource access. We therefore investigated clutch sex ratio in relation to social dominance for six years in colonial jackdaws.

Methods

Study population

We studied free-living jackdaws in the colony at the Zoological Laboratory in Haren (The Netherlands), a semi-urban environment. The data reported in this paper were collected in six years in the period from 1997 to 2005. Data on hatchling sex were not available for 1999, 2002 and 2003.

Nest boxes were checked daily, starting in the first week of April, until the clutch was complete, and eggs were numbered with a felt tip pen. To determine from which egg a chick had hatched, clutches were moved to an incubator 1–2 days before the estimated hatching date (temperature 37.7°C, humidity 75%). Clutches were exchanged for hard-boiled quail eggs, which were readily accepted and incubated by the jackdaws. Length and width of the eggs were measured to the nearest 0.1 mm, and egg volume (V , in cm^3) was estimated using the formula: $V = (\pi * A_2 * L * K) / 6$, where A is

width, L is length and for jackdaws $K = 0.00096$ (Soler 1988). Eggs in the incubator were checked at least every 2 h during daytime (from dawn until dusk) and hatchlings were immediately placed in the nest and quail eggs were simultaneously removed. It is unlikely that using an incubator affected hatching success, as the eggs were only in the incubator for the last 1–2 days of the total incubation period (± 18 days) (Salomons et al. 2006). Before being placed in a nest, the hatchlings were weighed and a blood sample (10–20 microlitre) was taken by clipping the tip of a toenail for sexing and future DNA-analysis. The clipping of a nail does not interfere with nestling growth. The clipped nail is identifiable by a blunt tip up to fledging, and we used this to identify the chicks within broods.

The survival of the chicks in the nest was checked every 5 days (hatch date of the first egg = day 1). At day 10, 20 and 30 the chicks were also weighed and tarsus- and wing length (day 20 and day 30) were measured. At day 30, shortly before fledging, the chicks were ringed. Breeding birds were individually marked with colour rings and a metal numbered ring. Birds were caught before the breeding season in a large baited cage or in their nest box using trap doors before or during breeding. Early in the nestling period (day 5) a sample of adults was captured in 1998 and most breeding birds were captured at that stage in 2000, 2001, 2004 and 2005. Biometric characteristics (tarsus and wing length, mass) were measured, a small blood sample was taken for DNA using puncture of the brachial vein, and as a rule birds were released within 20 min after capture.

Sex determination

Sex was determined by PCR analysis of blood samples (Griffiths et al. 1998). The reliability of this method was confirmed using adult birds of known sex ($N > 50$). All unhatched eggs were checked for embryos (except for 1997). In total 35 embryos were recovered, of which we were able to sex 32 (91%). Sex ratio among

unhatched embryos was female biased (21 females, 11 males), however this bias was not significant (binomial test: $P = 0.1$). In all sex ratio analyses the hatchlings and unhatched embryos were pooled.

Dominance

Agonistic interactions were recorded during March and the first half of April in 1998, 2000, 2004 and 2005, until the first egg in the colony was laid. To stage conflicts, food was offered in small pits (Ø10 cm) approximately 10 m from the nearest nest box. For further details see Verhulst and Salomons (2004).

The success in agonistic interactions of an individual bird was calculated using “David’s score” (David 1987; Gammell et al. 2003). This equation takes both the proportion of interactions won and the proportion of individual birds supplanted into account (other methods to calculate rank from these data yielded almost identical results). Based on the success score, a rank number was assigned to each bird. For each year we then scaled rank between 0 and 1 (most and least dominant male respectively) because the number of birds in the hierarchy differed slightly between years.

Male jackdaws are dominant over females, and the females’ success in conflicts is highly dependent on the rank and proximity of her partner (Lorenz 1931; Röell 1978; Wechsler 1988). Consequently we cannot determine female rank independently, and used the rank of the male to characterize the pair.

In 1997 and 2001 insufficient data on social status were collected to assign dominance ranks. Since the hierarchy within the colony was highly stable over several years (Röell 1978; Verhulst & Salomons 2004 Salomons et al, unpublished results), we used the dominance rank recorded in 1998 for 1997, and the dominance rank observed in 2000 for 2001. Note that insofar we erred in assigning dominance rank in this way this makes statistical tests of the effect of dominance on sex ratio and other traits more conservative.

Statistical analysis

A number of individuals were sampled in multiple years, and different breeding attempts from the same individuals cannot be considered independent samples. To avoid pseudo-replication we analyzed the data with a repeated measures hierarchical linear model, using the program MLwiN (version 2.02) (Rasbash et al. 2000). We used identity of the mother and breeding attempt (nested within mother) as random effects. Binary data (offspring sex) were transformed by the logit link function and analyzed assuming a binomial error distribution on the individual level. Statistical significance of variables was assessed from the increase in deviance (ΔDev) when the variable was removed from the model. The change in deviance is asymptotically distributed as χ^2 with corresponding change in degrees of freedom (Snijders & Bosker 1999).

Results

Overall sex ratio for the six years combined did not deviate significantly from 50% (51.3% males, $N = 489$, binomial test $P > 0.05$), and the clutch sex ratio distribution did not differ significantly from a random binomial distribution with $p_{\text{male}} = 0.5$ ($\chi^2 = 32.4$, $df = 26$, $P = 0.18$).

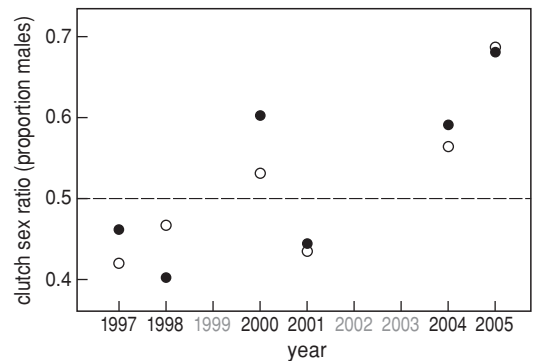


Figure 7.1. Annual sex ratio in the population (closed dots), and for the subset of birds with known dominance rank (open dots).

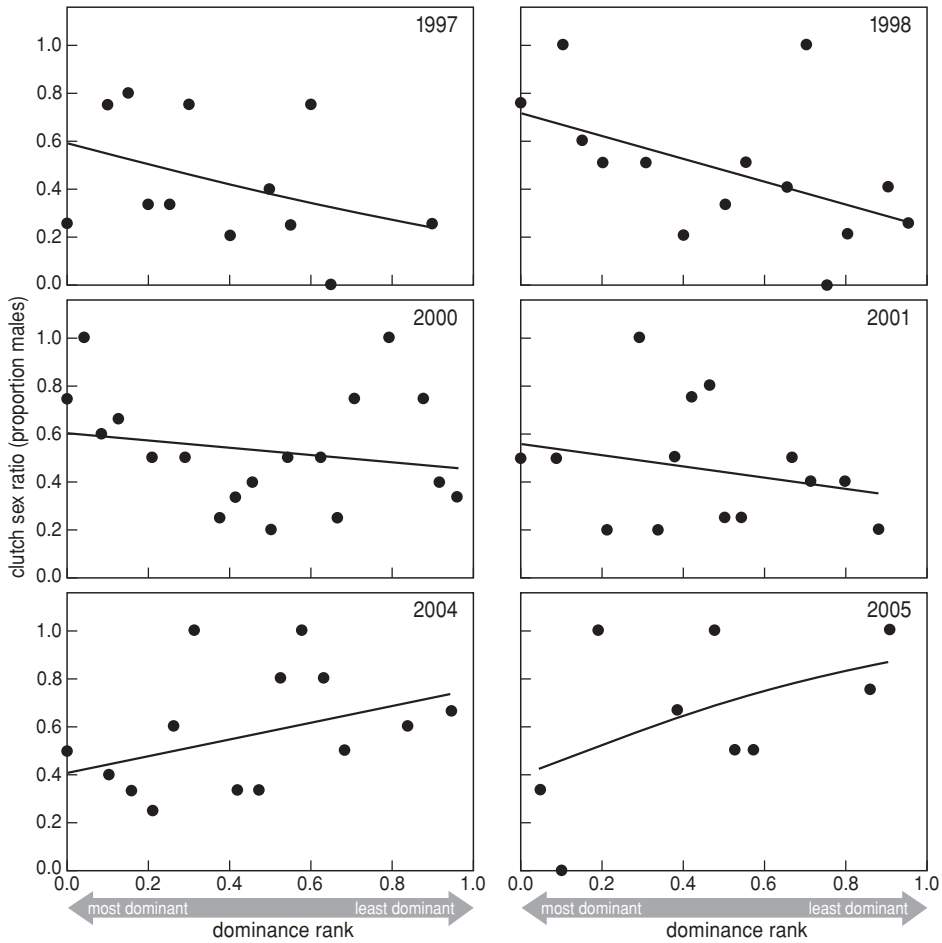


Figure 7.2. Social dominance and clutch sex ratio in six seasons from 1997 to 2005. For statistics see table 1. Each dot represents one clutch.

However, the overall sex ratio differed significantly between years (Fig. 7.1; $\Delta\text{Dev} = 16.35$, $df = 5$, $P = 0.005$). The subset of birds of which the dominance rank was known (68%) showed the same pattern, although due to the reduction in sample size the difference between years did not quite reach significance (Figure 7.1; $\Delta\text{Dev} = 8.55$, $df = 5$, $P = 0.1$).

Social dominance was related to sex ratio (Figure 7.2), but the direction of this correlation varied significantly between years (Table 7.1). To explore the cause of the variation between

years it is useful to first identify in more detail which (groups of) years were similar to each other, and which (groups of) years differed from each other. Based on the slope of the relation between dominance rank and sex ratio in the different years (Table 7.1), we created a model with either two year-groups (group 1: 1997, 1998, 2000 & 2001; group 2: 2004 & 2005) or three year-groups (group 1: 1997 & 1998; group 2: 2000 & 2001; group 3: 2004 & 2005). We tested these models against the original model (all years separate) using the Akaike Infor-

mation Criterion (AIC). The model with two year-groups emerged as the best fitting model (Figure 7.3; Table 7.1); more complicated models did not yield a significant increase in the explained variation. This was further confirmed by the finding that within the two year-groups the slopes did not differ significantly between years. In both year-groups the slope of the relation between social dominance and brood sex ratio was significantly different from zero.

(group 1: $\Delta\text{Dev} = 4.508$, $df = 1$, $P = 0.03$; group 2: $\Delta\text{Dev} = 4.830$, $df = 1$, $P = 0.03$). These results did not change, for example the slopes are almost identical (Table 7.1D), when data from 1997 and 2001 (in which dominance was not measured directly) were removed from the analysis.

In many avian species chick survival probability decreases with laying order (Dijkstra et al. 1990a; e.g. Badyaev et al. 2002), and this pattern is also evident in jackdaws (Gibbons 1987).

Table 7.1. Statistical analysis of the relation between social dominance and clutch sex ratio.

Model	Variables	Estimates (SE)						Rank*Year or Year-group	AIC
A	Year	1997	1998	2000	2001	2004	2005	$\Delta\text{Dev} = 11.54$ $df = 5$ $P = 0.042$	478.95
	N	13 / 50	14 / 60	19 / 75	15 / 62	16 / 53	9 / 32		
	Constant	0.39 (0.56)	0.88 (0.55)	0.48 (0.46)	0.17 (0.53)	-0.54 (0.57)	-0.14 (0.75)		
	Rank	-1.88 (1.26)	-2.04 (0.96)	-0.61 (0.82)	-0.99 (1.06)	1.71 (1.05)	2.07 (1.48)		
B	Year-group	1997 & 1998		2000 & 2001		2004 & 2005		$\Delta\text{Dev} = 10.99$ $df = 2$ $P = 0.004$	473.93
	N	17 / 27 / 110		19 / 34 / 137		19 / 25 / 85			
	Constant	0.59 (0.38)		0.27 (0.34)		-0.38 (0.44)			
	Rank	-1.81 (0.73)		-0.69 (0.63)		1.80 (0.83)			
C	Year-group	1997 - 2001				2004 & 2005		$\Delta\text{Dev} = 9.34$ $df = 1$ $P = 0.002$	471.97
	N	29 / 61 / 247				19 / 25 / 85			
	Constant	0.41 (0.26)				-0.37 (0.44)			
	Rank	-1.17 (0.48)				1.78 (0.48)			
D	Year-group	1998 & 2000				2004 & 2005		$\Delta\text{Dev} = 8.89$ $df = 1$ $P = 0.003$	
	N	26 / 33 / 135				19 / 25 / 85			
	Constant	0.62 (0.34)				-0.40 (0.44)			
	Rank	-1.24 (0.60)				1.90 (0.86)			

Results were analysed without pooling years into groups (A), pooled into three year groups (B) or into two year groups (C). Sample sizes are shown for the different levels of the analysis, number of females, number of nests and number of chicks respectively (jackdaws produce one clutch per year, therefore number of nests is not shown for A). Different models were compared using the Akaike Information Criterion (AIC). Years were pooled based on the slope of the relation between social dominance and sex ratio (model A). Of the three models, model C has the lowest AIC value and is therefore considered the best model. Results did not change after removal of data from 1997 and 2001 (D).

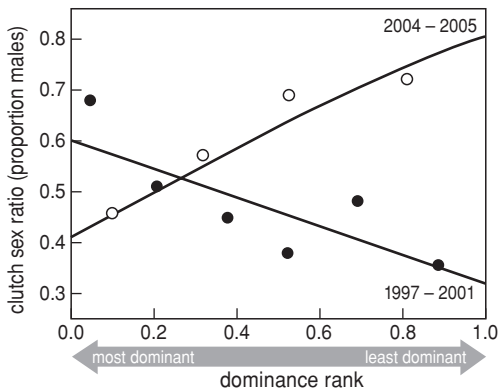


Figure 7.3. Social dominance and sex ratio in two year-groups. Data were pooled for 1997, 1998, 2000 and 2001 (solid dots, each dot represents 9 or 10 clutches, $N = 58$) and 2004 and 2005 (open dots, each dot represents 5 or 6 clutches, $N = 23$) respectively. For statistics see table 7.1.

When sex ratio adjustment is costly it is to be expected that such adjustment is most pronounced in eggs early in the laying order, since the potential benefits will be highest for eggs laid early in the clutch. Analyses of effects of laying order are complicated by variation in clutch size (should the third egg of a three egg clutch be compared to the third or the fifth egg of a five egg clutch?). We chose to assign eggs to one of three categories: first egg, last egg, and all 'middle' eggs. The sex of a chick was independent of laying order ($N = 489$, $\Delta\text{Dev} = 1.67$, $df = 2$, $P = 0.43$). More importantly, we found no interaction between social dominance and laying order in relation to offspring sex in either of the year-groups (1997-2001, $N = 247$, $\Delta\text{Dev} = 1.90$, $df = 2$, $P = 0.39$, 2004-2005, $N = 85$, $\Delta\text{Dev} = 0.13$, $df = 2$, $P = 0.94$, Figure 7.4). Thus we conclude the effect of social dominance on sex ratio was equally strong in all eggs of a clutch.

To investigate the cause of the change in slope from the first to the second year group we first tested whether the change was present within individuals or, alternatively, could be explained by a change in colony composition over time. There are nine individual females for

which information on sex ratio and pair dominance rank was available for both year groups. Unfortunately, this sub-sample was too small to allow for a reliable analysis using (binomial) hierarchical linear models. Therefore, we calculated the expected change in clutch sex ratio, based on our regression model (Table 7.1C), for these individuals from the first year group to the second year group, taking into account the (generally small) changes in dominance rank, and plotted the expected change against the observed change in clutch sex ratio. If the change in slope between year groups (Figure 7.3) was due to changes in population composition we would expect no correlation between predicted and observed change in sex ratio. In contrast, if the change in slope between year groups was due to some environmental effect on the whole colony we would expect a correlation between observed and expected change in sex ratio with a slope of 1. The slope of the regression line was indeed very close to 1 (slope = 0.84; Figure 7.5), suggesting that the observed change in the relation between social dominance and clutch sex ratio over time also occurred within individuals, although it should

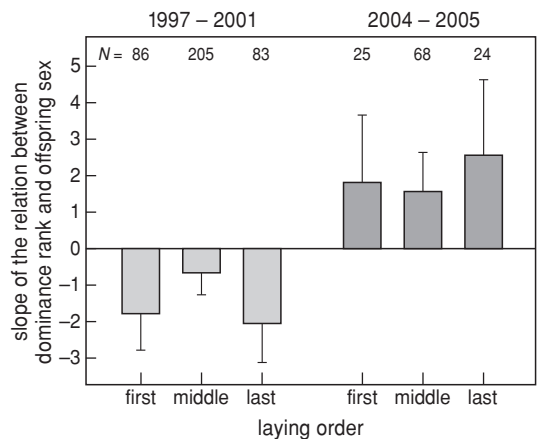


Figure 7.4. The slope (\pm s.e.) of the relation between dominance rank and offspring sex in relation to laying order in the two year-groups (1997-2001 and 2004-2005). Numbers above the bars indicate sample sizes (number of sexed offspring).

be noted that, perhaps due to the small sample size, the relationship did not reach significance ($r_9 = 0.53$, $P = 0.1$). Nevertheless, because the slope of the relationship between observed and expected change was approximately 1, we consider a temporal change in the environment as opposed to a change in the population composition the most parsimonious explanation for the change in slope between year groups.

Given that this change in the relationship between social dominance and sex ratio indeed occurred within individuals, this implies that there was another mediating factor affecting sex ratio which interacted with social dominance and has changed over time. Based on the literature we selected two factors that were repeatedly shown to be associated with clutch sex ratio, namely parental condition (Nager et al. 1999; Pike 2005) and laying date (Dijkstra et al. 1990b; Arnold & Griffiths 2003). We used body mass (residual of regression of mass on tarsus ($\Delta\text{Dev} = 62.1$, $P < 0.001$)) as an index of parental condition, and retained tarsus in the model as index of body size. Neither male residual mass, nor female residual mass measured during the breeding season (when nestlings were 5 days old) was correlated with clutch sex ratio (Table 7.2). The same (lack of) result emerged when we tested the effects of residual mass measured before the breeding season (data available for 2004 and 2005 only; Table 7.2). For neither measurement was there a significant interaction with year or year group. As a second estimate of parental (maternal) condition we used egg volume, which was previously shown to be correlated with female condition and subsequent reproductive success (Verhulst & Salomons 2004). There was no difference in the size of an egg containing a male or a female embryo (males: $10.52 \pm 0.08 \text{ cm}^3$, females: $10.65 \pm 0.08 \text{ cm}^3$; for statistics see table 7.2), and clutch sex ratio was not correlated with mean clutch egg volume. Females high in social rank laid smaller eggs in all years of this study, and there was no significant interaction between social dominance and year group (Table 7.2).

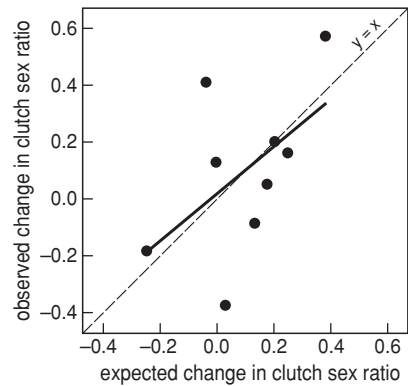


Figure 7.5. Observed change in clutch sex ratio within nine individual females between the two year-groups (1997–2001 and 2004–2005) plotted against the expected change based on the model in Table 7.1C. The solid line shows the linear regression through these points while the dotted line indicates equal values.

Sex ratio increased significantly with laying date ($N = 489$ chicks, $\Delta\text{Dev} = 4.0$, $df = 1$, $P < 0.05$). However, visual inspection of the regression results (Figure 7.6) showed that this effect was present in one year only (2000) whereas sex ratio was largely independent of laying date in the other years. This difference in the effect of

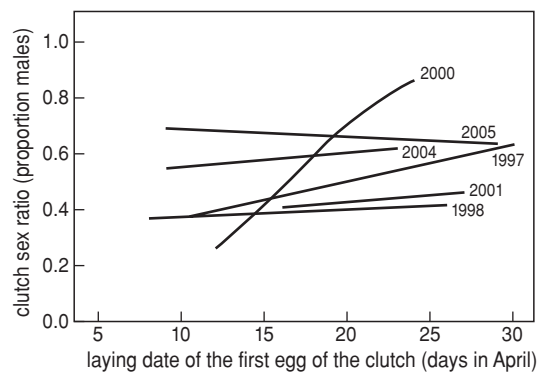


Figure 7.6. Clutch sex ratio as a function of laying date (number of days from the 1st of April) of the first egg of a clutch for the six years of this study. Shown are fitted lines for each of the years plotted over the date range that clutches were produced in these years.

Table 7.2. Statistical analysis of the effect of various factors on clutch sex ratio.

Independent	Year-group	Variables	Estimates (SE)	Statistics (<i>df</i> = 1)
Effect of maternal condition and size before the breeding season	All years <i>N</i> = 29 / 39 / 147	Constant	-2.780 (7.424)	$\Delta\text{Dev} = 0.125$ $P = 0.72$
		Residual mass	-0.006 (0.018)	$\Delta\text{Dev} = 0.185$ $P = 0.67$
		Tarsus	0.073 (0.170)	
	1997 - 2001 <i>N</i> = 14 / 17 / 73	Constant	-3.178 (7.793)	Interaction with year-group $\Delta\text{Dev} = 0.036$ $P = 0.85$
		Residual mass	-0.007 (0.028)	
		Tarsus	0.077 (0.178)	
	2004 - 2005 <i>N</i> = 20 / 22 / 74	Constant	-2.708 (7.792)	
		Residual mass	-0.014 (0.027)	
		Tarsus	0.077 (0.178)	
Effect of paternal condition and size before the breeding season	All years <i>N</i> = 31 / 38 / 141	Constant	9.147 (6.756)	$\Delta\text{Dev} = 0.631$ $P = 0.43$
		Residual mass	-0.016 (0.020)	$\Delta\text{Dev} = 1.540$ $P = 0.21$
		Tarsus	-0.184 (0.148)	
	1997 - 2001 <i>N</i> = 15 / 16 / 63	Constant	14.043 (7.268)	Interaction with year-group $\Delta\text{Dev} = 1.980$ $P = 0.16$
		Residual mass	-0.049 (0.034)	
		Tarsus	-0.283 (0.157)	
	2004 - 2005 <i>N</i> = 20 / 22 / 78	Constant	13.166 (7.078)	
		Residual mass	0.013 (0.027)	
		Tarsus	-0.283 (0.157)	
Effect of maternal condition and size during the breeding season	All years <i>N</i> = 42 / 85 / 327	Constant	1.104 (4.383)	$\Delta\text{Dev} = 0.031$ $P = 0.86$
		Residual mass	0.003 (0.016)	$\Delta\text{Dev} = 0.049$ $P = 0.82$
		Tarsus	-0.022 (0.100)	
	1997 - 2001 <i>N</i> = 34 / 57 / 226	Constant	1.614 (4.269)	Interaction with year-group $\Delta\text{Dev} = 0.062$ $P = 0.80$
		Residual mass	0.001 (0.021)	
		Tarsus	-0.040 (0.098)	
	2004 - 2005 <i>N</i> = 21 / 28 / 101	Constant	2.443 (4.293)	
		Residual mass	0.008 (0.023)	
		Tarsus	-0.040 (0.098)	
Effect of paternal condition and size during the breeding season	All years <i>N</i> = 37 / 72 / 279	Constant	11.695 (5.206)	$\Delta\text{Dev} = 4.918$ $P = 0.03$
		Residual mass	-0.013 (0.018)	$\Delta\text{Dev} = 0.517$ $P = 0.47$
		Tarsus	-0.253 (0.114)	
	1997 - 2001 <i>N</i> = 24 / 44 / 178	Constant	9.510 (5.164)	Interaction with year-group $\Delta\text{Dev} = 0.247$ $P = 0.62$
		Residual mass	-0.017 (0.020)	
		Tarsus	-0.211 (0.113)	
	2004 - 2005 <i>N</i> = 21 / 28 / 101	Constant	10.312 (5.134)	
		Residual mass	0.002 (0.034)	
		Tarsus	-0.211 (0.113)	
Effect of egg volume	All years <i>N</i> = 56 / 126 / 478	Constant	-0.232 (1.065)	$\Delta\text{Dev} = 0.086$ $P = 0.77$
		Egg volume	0.029 (0.099)	
		Tarsus	0.250 (1.232)	Interaction with year-group $\Delta\text{Dev} = 0.303$ $P = 0.58$
	1997 - 2001 <i>N</i> = 46 / 94 / 364	Constant	0.250 (1.232)	
		Egg volume	-0.031 (0.115)	
		2004 - 2005 <i>N</i> = 25 / 33 / 117	Constant	-0.414 (2.056)
Egg volume	0.091 (0.189)			
Tarsus	-0.211 (0.113)			
Effect of clutch size	All years <i>N</i> = 57 / 127 / 489	Constant	0.132 (0.680)	$\Delta\text{Dev} = 0.008$ $P = 0.93$
		Clutch size	-0.013 (0.146)	
		Tarsus	0.211 (0.351)	Interaction with year-group $\Delta\text{Dev} = 0.457$ $P = 0.50$
	1997 - 2001 <i>N</i> = 46 / 94 / 372	Constant	0.130 (0.733)	
		Clutch size	-0.047 (0.157)	
		Clutch size	-0.383 (1.615)	
	2004 - 2005 <i>N</i> = 25 / 33 / 117	Constant	-0.383 (1.615)	
Clutch size		0.211 (0.351)		

Estimates are shown for all years combined and for the two year-groups. Only one estimate for the effect of tarsus is shown as there was no significant interaction between tarsus and year-group. Sample sizes are shown for the different levels of the analysis, number of females, number of nests and number of chicks respectively. Sample sizes differ between analyses due to missing values. *P*-values are given for the variables in the complete set as well as for the interaction of year-group with the variable of interest in the pooled dataset.

laying date on sex ratio in 2000 compared to the other years combined was significant ($N = 489$ chicks, $\Delta\text{Dev} = 7.0$, $df = 1$, $P < 0.01$). There was no correlation between social dominance and laying date, and no significant interaction between social dominance and year group.

Discussion

Effects of social dominance on sex allocation have repeatedly been demonstrated in mammals, and we provide what is to our knowledge the first direct evidence for dominance dependent sex allocation in birds. Social dominance (Henderson & Hart 1995; Verhulst & Salomons 2004) and sex allocation (Arnold & Griffiths 2003) are both important components in the life-history of jackdaws, and therefore it was not unexpected that these were related. However, the effect was very strong when compared to most avian sex ratio studies (West & Sheldon 2002), with a sex ratio difference of 30-40% between the most and least dominant pairs (Figure 7.3). What was further surprising was that there was a dramatic shift in the effect of social dominance on sex allocation in the course of the study (Figure 7.3). In the first four years social dominance was positively related to the proportion of sons, in agreement with the pattern generally found in mammals. However, in the last two years the relationship was reversed, with high ranked jackdaws producing more daughters and low ranking birds producing more sons. Thus we conclude that social dominance has a strong effect on sex allocation in jackdaws, but that the direction of this effect is variable.

Spatial or temporal variation in sex allocation in relation to a trait such as social dominance is difficult to detect. Nevertheless, there are other examples of studies showing spatial or temporal variation in sex allocation patterns. For example, significant interactions between year and ultraviolet coloration in relation to sex ratio variation have been reported for blue tits

(Badyaev et al. 2002; Griffith et al. 2003; Korsten et al. 2006), and variation in sex allocation patterns between different populations have been reported for house finches (Badyaev et al. 2002) and red deer (Kruuk et al. 1999). Although explanations for these kinds of variation are mostly absent, and some authors themselves even suggest methodical instead of biological causes, such studies nevertheless illustrate that sex allocation can be a subtle process, and also that data sets will need to cover a substantial amount of temporal and/or spatial variation to fully capture the sex allocation strategies employed.

To study the shift in the relation between social dominance and brood sex ratio between years more closely, we checked whether this effect was also found within individuals. Data from a subset of individuals that produced offspring in both year groups provided suggestive evidence that the relation between social dominance and sex ratio changed within individuals (Figure 7.5). Consequently, it is unlikely that our results were caused by a change in colony composition. This implies that there is at least one other factor that affects sex allocation and its relation to social dominance.

The main criterion that this unknown factor should fulfill is that it should be related to sex ratio and social dominance, and that the relation with social dominance differed between the two year groups. We tested two candidates: laying date and parental condition. Laying date was recently shown to correlate with clutch sex ratio in jackdaws, with later clutches containing progressively fewer sons (Arnold & Griffiths 2003). Surprisingly, the jackdaws in our population showed the opposite pattern, with broods produced late in the season containing on average more sons, although this effect was largely due to one year (Figure 7.6). More important in the present context is that laying date was not related to social dominance in either year group or overall, and there was no interaction between social dominance and year group with respect to laying date. Thus we

conclude that the shift in effect of social dominance on clutch sex ratio was not mediated by effects of timing of breeding.

The second candidate was parental condition. Previously it was shown in the same colony that social dominance negatively affected female condition during the breeding season of 1998 and 2000 (Verhulst & Salomons 2004). This was reflected in both a lower body condition (residual mass over tarsus) at day 5 of the chick stage, and in the smaller size of the eggs laid by females that were paired to dominant males. Analyses of the larger data set now available confirmed these earlier findings, but found no evidence for a significant interaction between social dominance and year group on maternal condition. Furthermore, when using residual body mass and egg volume as indices of female and male condition we found no evidence for condition dependent sex ratio in our study. We conclude therefore that the shift in effect of social dominance on clutch sex ratio was not mediated by (our measures of) parental condition.

An alternative explanation is that the relation between brood sex ratio and social dominance, and the observed shift in this relationship, is mediated by maternal hormones which are in turn affected by environmental changes. Both testosterone and corticosterone make good candidates for such mediating effects. The relation between social dominance and testosterone has been shown to interact with the environment (i.e. population density and stability of the social hierarchy (Schwabl 1997; Rogovin et al. 2003), while corticosterone level is known to depend on stress and body condition (Kitaysky et al. 1999; Cyr & Romero 2007). Furthermore, broods produced by females with high levels of testosterone were found to be male biased in Japanese quail (Pike & Petrie 2005a) and experimentally increased maternal levels of testosterone resulted in an increase in brood sex ratio in the zebra finch and the spotless starling (Veiga et al. 2004; Rutkowska & Cichon 2006), but not in Japanese quail (Pike &

Petrie 2006). Similarly, corticosterone has been shown to reduce brood sex ratio in peafowl and Japanese quail (Pike & Petrie 2005a; Pike & Petrie 2006). Unfortunately, we have not yet measured hormone levels in this study. The number of breeding pairs however has slightly decreased in recent years, suggesting that relevant environmental circumstances (e.g. breeding density) have changed. Indeed there was a trend that the number of breeding pairs is correlated with the slope of the relation between social dominance and brood sex ratio ($r_s = 0.64$, $N = 6$, $P = 0.054$). We will gather more data on this since the sample size is at present too low to allow firm conclusions.

We attempted to understand the shift in effect of social dominance on clutch sex ratio from a mechanistic perspective (Hogan 2005) by investigating correlations of clutch sex ratio with factors known to affect sex allocation in other species. Alternatively, one could analyze how the fitness prospects depend on clutch sex ratio for birds with different social dominance, which could yield an understanding of the observed shift from a functional perspective (Cuthill 2005). However, life histories of birds and mammals are often very complex, making it difficult to derive predictions regarding the optimal sex ratio with confidence (Komdeur & Pen 2002; West et al. 2002). In this context, spatial or temporal variation in the effect of a trait on clutch sex ratio as found in this study may be an asset, because it creates the opportunity to make multiple comparisons between predictions and observations within one study system. Furthermore, predictions regarding temporal or spatial differences in sex allocation within study systems are likely to be more accurate than predictions for single values, since one can reasonably hope that inaccuracies in parameter values will affect all estimates in the same way (provided there are no strong interactions with these parameters). Nonetheless, the cause of the shift in the effect of social dominance on sex ratio in this study remains an open question at present, and the

number of study years will probably have to increase before this can be resolved.

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