

Extra-pair paternity in the Skylark *Alauda arvensis*

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We present the first quantitative data on the genetic breeding system of a lark (Alaudidae), the Skylark *Alauda arvensis*. Using a set of eight microsatellite loci isolated in a variety of passerine species, we genotyped 171 offspring from 52 broods of Skylark and detected 35 extra-pair offspring (20%), in 14 different broods (27%). All offspring matched their putative mother, so there was no evidence of intraspecific brood parasitism. Previous non-genetic studies had suggested that the species was predominantly socially monogamous, with only rare occurrences of social polygyny and polyandry, although some behaviours, such as mate guarding, did suggest the possibility of extra-pair copulations. The relatively high level of extra-pair paternity in this species is likely to affect the variation in male reproductive success because extra-pair paternity was non-randomly distributed amongst males, with those with shorter wings more likely to be cuckolded.

Keywords: Alaudidae, cuckoldry, wing length

It is now commonly accepted that mating systems cannot be easily predicted from observations of social behaviour. Amongst socially monogamous bird species surveyed by molecular methods, true genetic monogamy occurs in less than 25% and on average over 11% of offspring are not sired by the male that attends the nest (Griffith *et al.* 2002). Over a hundred bird species have now been investigated with molecular methods to determine levels of extra-pair paternity. Nevertheless our understanding of the function of extra-pair paternity remains limited: while males can substantially increase their reproductive success by siring extra-pair offspring, (e.g. Trivers 1972, Sheldon & Ellegren 1999, Whittingham & Dunn 2005), why females participate in extra-pair copulations is not so obvious. Numerous hypotheses have been proposed (Petrie & Kempenaers 1998, Griffith *et al.* 2002, Westneat & Stewart 2003) but insightful tests of these hypotheses are rare.

Most of our understanding of extra-pair paternity (EPP) has come from comparative studies that have investigated the relationship between interspecific variation in the incidence of EPP and, for example, plumage colouration and brightness (Møller & Birkhead 1994, Owens & Hartley 1998), breeding density (Westneat & Sherman 1997), population insularity (Griffith 2000), and need for parental care (Møller 2000, Arnold & Owens 2002). One finding is that nearly 60% of interspecific variation in the level of EPP occurs between families or orders, rather than between closely related species (Arnold & Owens 2002, Bennett & Owens 2002, Griffith *et al.* 2002). Therefore future comparative work will particularly benefit from data on higher-level taxa under-represented in the current data. Even in passerines, the most extensively worked order, while some families are represented by estimates from numerous species (e.g. Fringillidae, Hirundinidae, Paridae), in many families no representatives have been investigated. Our study is the first quantitative estimate of the level of EPP in a lark (Alaudidae), the Skylark *Alauda arvensis*.

The only other study of extra-pair paternity in the Alaudidae concerned two species of *Calandrella* in Spain (Sánchez *et al.* 2004). Although only two families of the Short-toed Lark (*C. brachydactyla*) and one family of Lesser Short-toed Lark (*C. rufescens*) were successfully analysed, in both species there was evidence of one chick not being the offspring of a male caught at its nest. But in two out of 23 families of Lesser Short-toed Larks, two different males were caught feeding the chicks, and in a third family in which the male died a second male fed the chicks. So it may be that this species is regularly polyandrous, in which case the genotyped chick need not necessarily have been extra-pair. The lack of good data on putative parentage and the sample of only three families from two species, limit the conclusions that may be drawn from Sánchez *et al.*'s (2004) study. We see the primary purpose of our paper in providing future comparative analyses with a solid data point for Alaudidae, but knowledge of the EPP rate in skylarks should also aid interpretation of this species' social behaviour.

The Skylark is territorial and generally socially monogamous, with the male not helping in nest construction or incubation, but contributing up to half the chick feeding, or even more after the chicks leave the nest (Delius 1963). Delius (1963) reported that of 93 monogamous pairs studied, none showed polyandry, and at least one of the two cases of polygyny involved a paired male deserting one female in preference for a widowed female and her territory (i.e. a serial process rather than true bigamy). Jenny (1990) reported a similar case of a male changing female and territory while his deserted partner was feeding chicks. (And such changes in partner occur frequently between breeding seasons, especially following below-average breeding success: Delius 1965). However, we also observed one case of a male sharing its territory with two different females simultaneously. Duncan (1987) observed an even clearer case of polygyny, which led to each female laying two or three clutches and the male at one time taking turns in feeding both their broods. Duncan (1987) also reported one possible case of polyandry, in which a female regularly associated with two neighbouring males both before and during incubation. P. Odderskær (pers. comm.) observed a case of three Skylarks repeatedly flying to the same nest at the chick-feeding stage (two were radio-tagged).

These behavioural studies thus suggest that social monogamy is the norm with exceptional cases of social polygyny and social polyandry. Copulation outside the pair bond has never been observed, although, as with many other birds (Westneat & Stewart 2003), within-pair copulations

are also rarely seen, leading to Delius' (1963) unsubstantiated assertion that one copulation suffices to fertilise a whole clutch. Nonetheless, some behaviours can be construed as having an extra-pair agenda. For example, Møller (1991) observed males regularly entering neighbouring territories and displaying sexually in front of non-mates. Indeed, Delius (1963) described a special "tank-courtship" behaviour of males that resembles the normal intra-pair courtship behaviour prior to copulation, but is mostly directed towards females other than the social partner; however, it was never observed to lead to copulation. When attempting to lure Skylarks with song playback, we observed that a stuffed lark beside the speaker would sometimes attract a paired female away from her onlooking mate and cause her to perform apparent copulation solicitation movements towards the mount (JMCH, pers. obs.).

The closeness with which males guard their partners prior to egg laying also suggests a threat of extra-pair copulation. However, even during periods of mate guarding, males continue their aerial song flights, which would seem to make the displayer vulnerable to cuckoldry. Aerial displays may last many minutes, typically taking place at an altitude of 120 m, and sometimes over 200 m (Hedenström 1995). At this height, even in the typical short-grassland habitat, it would seem easy to overlook intruding males, especially as they may walk unobtrusively into the singer's territory. Sometimes the territory owner abruptly curtails its aerial singing and dives down to attack an intruder. However, although chases around a territory are common, both sexes are often to be observed feeding within the "territory" mapped out by another male's song flight (e.g. Donald 2004 p. 95), and indeed the same trap at a baited site often caught males and females from more than one pair even in the breeding season (JMCH pers. obs.). Maybe the presence of rivals within a territory is tolerated or overlooked unless they adopt particular postures or behaviours or approach the female.

There has been little previous work on sexual selection in Skylarks, but the song flight surely must play a prominent role, especially as the plumage is drab and does not distinguish the sexes. Although rare female song flights have been reported by other authors (e.g. Delius 1963), in our study of colour marked birds intensively monitored for their singing behaviour we heard a female sing only when she was attacked by a Peregrine Falcon *Falco peregrinus* (see also Cresswell 1994). It is tempting to conclude that the 10% greater wing length of males is associated with their song-flight behaviour, especially as there is little within-population overlap between the sexes in this character and much more overlap in other measures of size such as mass and tarsus length (JMCH pers. obs., Delius 1963, Wolfenden 1989, Møller 1991, Dougall 1997, 1998). Although Hedenström & Møller (1992) did not find that passerine species with a male song flight had significantly greater sexual dimorphism in wing length or body mass, this was the case with wing span, wing area, wing loading, and aspect ratio. In agreement with this is Møller's (1991) finding that wing loading and aspect ratio correlated with the duration of a Skylark's song flight. Therefore we might expect that wing morphology, by affecting song-flight performance, may relate to a male's ability to maintain a territory and/or attract females, and thus potentially his ability to guard against cuckoldry and gain extra-pair offspring. Accordingly, our report includes a test of whether male wing length correlates with cuckoldry.

METHODS

Skylarks were studied at three locations, Lundy, an island of approximately 3 km² in the Severn Estuary, UK, and at Oldbury and Ashton Court, both near Bristol, UK. On Lundy, Skylarks bred on open heath and grassland grazed by sheep and density of territorial males in occupied habitat was about 30 km⁻². At Oldbury the habitat was a mixture of coastal marsh, grassland and arable fields; density varied across the site from about 14 to 30 km⁻². Ashton Court was open grassland forming a public golf course, and density was about 50 km⁻². At all three sites individuals were caught over several years, mostly using whoosh nets (over the nest, or baited with mealworms and grain, or using song playback), spring traps or drag netting in the winter. Birds were ringed with a numbered

metal band and a unique series of coloured plastic rings for individual visual identification. A small blood sample (10–20µl) was taken from the brachial vein of each adult and stored in 100% ethanol.

A number of measurements were also taken (wing chord; lengths of primaries 3 and 7, tail, longest crest feather, tarsi, and hind claws; bill length and height; mass: methods follow Svensson 1992). To avoid a reduction in statistical power, we wanted a single measure of size for this study and chose wing chord because it is a widely used such measure (Gosler *et al.* 1995); we avoided using mass because birds had been caught at various times of the year and with or without baiting. Another reason to choose wing chord is that it is the most sexually dimorphic character and thought liable to be affected by sexual selection on song flights (see above; wing loading might have been better in this respect—Møller, 1991—but could not be reliably estimated owing to the inconsistent circumstances of mass measurement). In 12 out of 52 broods, the male's wing-chord length was available only from a different year to the measure of paternity, but our data show that repeated measurements of wing chord across different years differed by a mean of only 0.8 mm ($N = 32$ different males, measured a mean of 1.8 moults apart; cf. 0.7 mm within years, $N = 18$) and there was no tendency for it to increase or decrease systematically ($t_{31} = 0.81$). Even amongst six males known to have been measured in their first adult plumage (i.e. after a full moult in their first autumn), the mean increase in subsequent years was a non-significant 0.6 mm ($t_5 = 1.66$, $p = 0.16$).

Pairs were monitored for signs of breeding throughout the season at Oldbury and Ashton Court, but on Lundy for only a two- or three-week period each year (late June and early July), thus missing the first breeding attempts. Blood samples were taken from chicks when they were ringed in the nest. In most broods (44 of 52) putative fathers were either caught on the nest while feeding chicks or were observed feeding the chicks at that nest and identified by their colour rings. This criterion may introduce some bias because males evidently differ considerably in how bold they are about approaching the nest in the presence of an observer or of a whoosh net set around it, and it is possible that this readiness to feed the chicks correlates with their confidence in their paternity (cf. Sheldon & Ellegren 1998). So we also included eight broods, distinguished in the main analyses below, where the putative fathers were persistently observed in the territory containing the nest, so would normally be classed as paired to the female, but were not observed actually visiting the nest. In some of these eight broods such evidence is supported by observations of mate guarding the mother or of evidence of collecting food to feed chicks at the time that the chicks in this particular nest were being fed. In seven different broods the putative mother was not caught or identified delivering food to the nest, but since it turned out that maternity was always confirmed, we do not distinguish these broods.

There were only two cases where we had data on two broods from the same pair of parents (one case in separate years and one within the same year). Also some individual parents reappear in our data paired to different partners (the 52 broods involved 40 different social fathers and 44 mothers, none considered more than three times). We used all broods to calculate best estimates of EPP levels, but to calculate confidence limits and perform significance tests we avoided pseudoreplication by including only one brood from each parent (selected to maximise the number of broods and chicks remaining in the dataset).

Although all adults had been sexed based on morphological features measured at the time of capture (presence of a brood patch or cloacal protuberance, or—less reliably—wing length) and/or on their behaviour once colour ringed (e.g. only females incubate, only males normally sang), sex of all adults was confirmed using a molecular marker (Griffiths *et al.* 1998) to ensure that possible EPP was not misinterpreted as quasi-parasitism (see Griffiths *et al.* 2004).

Microsatellite-based genotyping was employed to investigate parentage using a suite of loci previously isolated in other passerines. Eighteen loci were initially screened for amplification and polymorphism in six random adults from the Lundy population. From these, eight loci were used for the molecular study (Table 1). For each locus, the polymerase chain reaction (PCR) was carried out in a Perkin Elmer model 9700 thermal cycler using the following PCR profile: an initial hot-start for 2 min at 94°C, followed by 5 cycles of 60 s at 94°C, 60 s at the annealing temperature (which varied between 52° and 56°C across loci), and 60 s at 72°C. This was followed by 30 cycles

with the same three steps but with each stage lasting for 30 s. Each 10 μ l mix included 0.1 unit of *taq* polymerase (Applied Biotechnologies), 8 μ l of Jeffreys' buffer (final concentration: 20nM (NH₄)₂SO₄, 75 mM Tris-HCl pH 8.8, 0.15 mg/ml DNase free BSA, 10mM β -mercaptoethanol, 2.5 mM MgCl₂; Jeffreys *et al.* 1988), 0.8 μ M of each primer and approximately 10 ng genomic DNA. Genomic DNA was prepared for the PCR using a simple Chelex resin-based extraction method (Walsh *et al.* 1991). Products were resolved in a vertical 6% denaturing polyacrylamide gel run in an S2 gel rig (BioRad), and visualised using silver-staining.

All individuals in a family were run alongside so that alleles could be compared directly. In addition, a 10 base-pair marker (Invitrogen) was run in three lanes on each gel to allow alleles to be sized (Table 1). Given the co-dominant nature of microsatellite loci, parentage was assigned simply on the basis of alleles shared with the mother and father.

RESULTS

In total, 171 offspring from 52 broods were genotyped with both their putative parents. In every case the genotypes of the offspring matched one of the maternal alleles, implying that we had correctly assigned maternity; there is thus no evidence of either intraspecific brood parasitism or quasi-parasitism (Griffith *et al.* 2004). However, 35 offspring (20%) were determined to be extra-pair given the number of mismatches with their putative father. All of these 35 offspring mismatched their putative father at a minimum of two of the eight loci and on average at 3.71 loci (\pm 0.22 s.e.m.). The other offspring (136) matched both putative parents at all eight loci. 95% confidence limits for the percentage of extra pair offspring are 11–35% (using Efron's percentile bootstrap method based on randomly resampling broods, and selecting randomly each run amongst pseudoreplicated broods: Manly 1997 p. 39). If we exclude the eight broods lacking observations of the male directly feeding at the nest, the level is essentially the same with 26 of 144 (18%; 95% CL = 9–30%) offspring sired outside the pairbond.

The 35 extra-pair offspring came from 14 out of a total of 52 broods (27%; 95% CL = 17–40%). Again, removing the eight broods where the male was not seen to feed the chicks scarcely changes the level of EPP (11 out of 44 = 25%; 95% CL = 16–42%). Overall, seven of the 52 broods showed mixed paternity (within-pair and extra-pair offspring) and in a further seven, all genotyped offspring were sired by an extra-pair male. The latter figure seems a high proportion, but bear in mind that we often have data on only two or three offspring per brood (mean = 3.3 overall and 2.7 for broods that are all extra-pair); mostly this is because of naturally small broods, and is only slightly compounded by 5 chicks from 5 broods not being successfully genotyped. Of course the same factor also means that females mating equally often with two males could easily by chance show up as faithful. Three of the seven broods that were all extra-pair came from the eight broods where the male was not confirmed to feed the chicks. These should not be lightly dismissed as cases of us misidentifying social partners: in all three cases the male's territory clearly included the nest, in one case there was also good evidence that he was feeding chicks at the time that this brood was being fed, in another case he was observed mate guarding the mother the week before egg laying.

Levels of EPP were similar in the two populations for which we have adequate data, Lundy and Oldbury, both at the family (30% and 25% respectively), and offspring level (21% and 24%) (Table 2). Similarly, levels seem reasonably consistent from year to year (Table 3). Our sample is sufficient to provide a reasonable estimate of the frequency of EPP, but there is a danger in making too many post-hoc comparisons between the levels of EPP and a number of male and female morphological traits. We therefore restricted ourselves to testing only for an effect of male wing-chord length. In the Lundy sample, shorter-winged males were significantly more likely to be cuckolded ($t_{14} = 2.3$, $N = 29$, $p = 0.038$, slightly increasing in significance to $p = 0.025$ if we exclude broods where the male was not identified feeding chicks; Fig. 1). Wing-chord length depends on both the length of feathers and the length of skeletal elements in the wing, so, as a follow up, we then examined whether EPP correlated more closely with the first principle

component of a collection of feather traits (primaries 3 and 7, tail, crest feathers) or of skeletal characters (tarsus lengths, and bill length and height). Both relationships were similarly weak. The Oldbury sample had only three broods containing extra-pair young, but their social fathers show no tendency to be smaller, and combining the two sites in one analysis drops the significance ($F_{1,34} = 1.09, p = 0.3$). Our view of the effect of wing length is that it is highly suggestive, and would not be surprising, but that it requires a replication to be fully convincing.

DISCUSSION

As with so many other species of passerine, social monogamy in the Skylark does not always result in genetic monogamy. Indeed the level of EPP in our sample (20% offspring) is above the mean for socially monogamous birds (11% offspring; Griffith *et al.* 2002). It is also slightly higher than that in the Collared Flycatcher *Ficedula hypoleuca* (16% offspring), and in that species extra-pair paternity produced a dramatic shift in reproductive skew amongst males (Sheldon & Ellegren 1999). Our findings suggest that, although Skylarks are socially monogamous and rarely indulge in polygyny, sexual selection between males could be quite strong through paternity lost and gained.

An effect of wing length on EPP, if confirmed by further work, begs several questions about the mechanisms underlying it. In this species wing length does not change with age (see Methods). However, the effect could be one of overall body size, which has been found to be positively related to level of cuckoldry in several other passerines (e.g. Morton *et al.* 1990; Yezerinac & Weatherhead 1997). It need not result from female choice but simply from males being more willing to intrude into the territories of small males because fights are less risky. Males or females might assess male size directly (the typical male prancing display would tend to amplify this trait), but one obvious possibility is that aspects of the striking male song flight provide the cue. However, Møller (1991) reported significant effects of only wing loading and aspect ratio, not body or wing size, on Skylark song duration. (His trimming of wing feathers did decrease duration, but this is a crude and sudden manipulation that need not have the same consequences as natural variation in wing length.) It would be worthwhile to measure the direct dependence of EPP, both gained and lost, on song duration and frequency.

We have not attempted to identify the extra-pair fathers owing to the incomplete population sampling and presence of close relatives (due to appreciable natal philopatry) at our study sites. One possibility is that extra-pair fathers are mostly immediate neighbours, but there were also apparently unpaired (or widowed) males present; these could have large territories and long durations of aerial song (cf. Donald *et al.* 2003). In a radio-telemetry study, P. Odderskær (pers. comm.) tracked an unpaired male near newly established nests just before egg-laying. Maybe there were also non-territorial males sneaking around that would have been easy to overlook; Delius (1963) estimated 10% of his study population was non-territorial, and observed such males take over two territories of widowed females within a few days. Unfortunately identifying a high proportion of the extra-pair fathers may be difficult because Skylarks are a hard species to catch.

Skylarks live in a variety of habitats including coastal marsh, grazed grassland, arable fields and upland heathlands. Density varies considerably between habitats (Donald 2004, p. 59), which may affect the level of EPP, but it is plausible that the height of the vegetation and the complexity of the topography matters more, by affecting the ease with which intrusion and extra-pair courtship is hidden from the territory owner. Another relevant difference may be between natural habitats, where territories are rather stable through the breeding season, and many agricultural landscapes in which harvesting and the rapid growth of autumn-sown cereals lead to dramatic shifts in territorial configurations through the breeding season (Schläpfer 1988, Jenny 1990). This social disruption might plausibly increase the level of EPP, for instance by changing rankings of male quality, or by increasing the incidence of males roving through others' territories whilst prospecting for a new territory. It has been suggested that the rate of EPP is also liable to be affected by the synchrony of breeding attempts (Stutchbury & Morton 1995), although the evidence is inconclusive

(Weatherhead & Yezerinac 1998, Griffith *et al.* 2002); synchrony is greater in natural habitats than disturbed agricultural habitats and also shows differences within the season (e.g. in natural habitats, greater for early broods; Jenny & Weibel 2001). A large body of recent research has been concerned with how agricultural intensification has been responsible for a population decline of this species (reviewed in Donald 2004); it is possible that it has had additional consequences for reproductive strategies.

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Table 1. Characterisation of the eight microsatellite loci in 80 adults in the three populations.

Locus	Reference	Size range (bases)	No. of alleles	Observed heterozygosity
Ase48	Richardson <i>et al.</i> (2000)	225–233	6	0.75
Ase18	Richardson <i>et al.</i> (2000)	165–215	12	0.78
Dpu16	Dawson <i>et al.</i> (1997)	145–157	6	0.41
Fhu2	Ellegren (1992)	127–147	7	0.69
MJG8	Martinez <i>et al.</i> (1998)	74–100	13	0.53
Phtr1	Fridolfsson <i>et al.</i> (1997)	74–90	5	0.51
Pdoμ5	Griffith <i>et al.</i> (1999)	88–138	11	0.68
Pocc6	Bensch <i>et al.</i> (1997)	173–187	5	0.53

Table 2. Levels of extra-pair paternity in the three different populations.

Population	No. of broods	No. of broods with EPP	% EPP (brood)	No. of offspring	No. of extra-pair offspring	% EPP (offspring)
Lundy	37	11	30	123	26	21
Oldbury	12	3	25	38	9	24
Ashton Court	3	0	0	10	0	0

Table 3. Levels of extra-pair paternity in the Lundy population by year.

Year	No. of broods	No. of broods with EPP	% EPP (brood)	No. of offspring	No. of extra-pair offspring	% EPP (offspring)
1997	7	3	43	21	5	24
1998	10	4	40	36	10	28
1999	7	1	14	24	3	12
2000	13	3	23	42	8	19

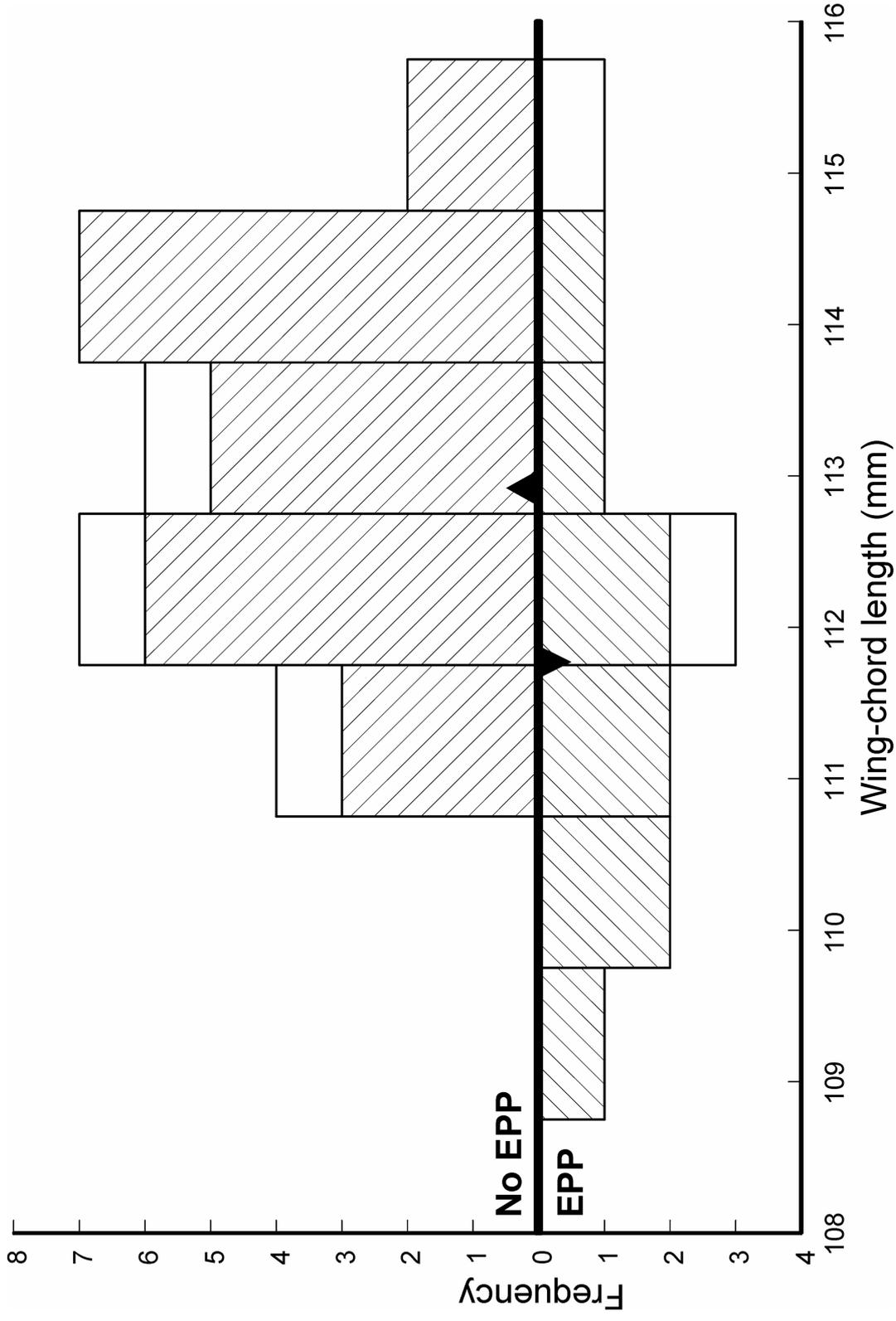


Figure 1. Wing-chord lengths of social fathers of those broods including an extra-pair chick (below line) and those without (above line). Triangles indicate means for each class. In this figure, but not in the statistical tests, some males appear more than once. The non-shaded components refer to broods where the father was not identified as it fed the brood.