

Lek-kin in birds — provoking theory and surprising new results

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I review studies relating to the question of whether kin selection is prevalent on leks and may help to explain their evolution. This is not a comprehensive review, instead my aim is to give an account of how kin selection became incorporated in lek research. I hope to show that theoretical modelling provoked empirical research, which in this particular case substantiated many of the theoretical predictions. However, some recent empirical studies have found results indicating kin clustering beyond what was anticipated by theory. The debate on the importance of kin selection and kin clustering in the case of leks is still in its infancy. New models and data will no doubt spur further research in this area.

Introduction

This is not an ordinary research paper. Instead my aim is to provide an account of how a particular piece of science has proceeded. Hopefully this story will give an insight into how scientific views change in the light of new results. I should stress that the paper is not to be read as a review or a full account of the state of affairs in this particular research field. The number of studies and data at hand are still too preliminary and scarce for this to be done. This being said, however, my present position and belief is that what we see emerging in this particular case will stand the test of time.

The particular story is the question of why, during the mating season, males in some species aggregate on so called leks to attract females. This is a research field that has gained interest in particular during the last 30 years (Wiley 1991,

Höglund & Alatalo 1995). In 1995, along with my colleague Rauno Alatalo, I published a book which was an extensive review on the subject (Höglund & Alatalo 1995). In that work, we attempted to review the hypotheses put forward to answer the above-mentioned question and scrutinize the empirical evidence in favour of each.

In our review, as well as those done by others, leks were thought of as prime examples of arenas for sexual competition (Bradbury 1981, Wiley 1991, Andersson 1994). Thus it was argued that good estimates of male fitness could be obtained by studying the variation in mating success among males in a population. The causes of the variation could then either be attributed to effects of mate choice (i.e. female preferences for particular kinds of males) or male-male competition (i.e. some males stop others from mating through direct or indirect competition). Although

the possibility of relatedness among males within leks had been briefly mentioned, to my knowledge, no one had raised the possibility that kin selection (*sensu* Hamilton 1964) could affect the variation in mating success among males, although the issue of whether displaying duos in long-tailed manakins (*Chiroxiphia linearis*) were related had been raised and rejected (McDonald & Potts 1994). Neither kin selection, relatedness nor inclusive fitness was indexed in our review (Höglund & Alatalo 1995). Could it be that if such an effect does occur, it could be important for understanding sexual selection and the evolution of leks?

In 1996, a theoretical paper suggesting that kin selection is indeed important for understanding these problems was published by Hanna Kokko and Jan Lindström (Kokko & Lindström 1996). In order to see the context of their work we need to make a small digression in to the sort of problems that occupied lek researchers at the time Kokko and Lindström's theoretical study appeared. In the late 1980s and early 1990s our research group concentrated on understanding how males should distribute themselves among a number of potential lek sites varying in size and number of females mating at each. In black grouse, *Tetrao tetrix*, we observed that lek size varied in our study area, and as a consequence a number of other important parameters varied as well (Alatalo *et al.* 1992). Most importantly, in our study the number of copulations per male increased approximately five-fold with increasing lek size. Furthermore, any given female visiting these leks was more likely to mate on larger rather than on smaller leks. This would indicate that large leks are always the best option for any given male. However, because matings are shared more evenly among males on larger leks, this is not always the case. In black grouse the returns in terms of mating success are about the same for an α -male (the most successful male on a lek) on a medium sized lek as for a β -male (the second most successful male on a lek) on a large lek. In ruffs, *Philomachus pugnax*, the optimal lek size is smaller for α as compared with that for β and smaller for β as compared with that for γ and so on (Widemo & Owens 1995). Thus lekking males seem to face a lek-choice problem: given competitive ability what size of lek is the

optimal choice? One important assumption in both the modelling of these sorts of problems and analyses of field data is that male fitness is driven by direct fitness, i.e. that our estimates of fitness, most often number of copulations, are directly related to number of offspring produced during life. We had shown that counting copulations is probably not affected to a large extent by cryptic copulations, sperm competition and other artefacts (Alatalo *et al.* 1996), but no one had calculated any possible inclusive fitness effects (Hamilton 1964).

Kin selection and black grouse

This is exactly what Kokko and Lindström did in their paper. In short, they derived distribution models of black grouse and ruffs under the assumption that males among leks were related (Kokko & Lindström 1996). Thus, they suggested the possibility that males unsuccessful in attracting and copulating with females still could have non-zero fitness if they were related, (i.e. shared genes by descent) with successful males. Among other things, this idea completely changes the prediction about optimal lek sizes for different kinds of males and of course an empirical test of this possibility was urgently needed.

Let me state that at the time I first read the Kokko and Lindström paper I thought it was provoking and interesting, but I was dead sure it was wrong and that it would be easy to prove it wrong. Fortunately, we had collected blood samples from a large number of males from many lek sites within our Finnish study area. Furthermore, PCR-primers developed for detecting microsatellite variation among red grouse (*Lagopus lagopus scoticus*) were starting to emerge (Piertney & Dallas 1997). Two of these proved to amplify reliable products in black grouse. To make a long story short, the microsatellite data suggested that males, but not females, were more related within leks than among leks, thus supporting the assumption used by Kokko and Lindström (Höglund *et al.* 1999). This was a completely surprising result which I actually found hard to believe. However, when thinking about the result and what

was known about the biology of black grouse at the time, this was in fact not surprising at all. Already in 1988 there were results pertinent to this study, and these results were obtained at the very same University at which I was then, and of which I am still a faculty member. Using radio-telemetry, Tomas Willebrandt showed that the average natal dispersal distance (the distance from place of birth to place of first reproduction) for females is about 20 km. For males, the same distance is 0 km, meaning that males essentially lack natal dispersal (Willebrandt 1988). Furthermore, it has long been known that outside the breeding season black grouse live in social units called winter-flocks (Klaus *et al.* 1990). These comprise birds of both sexes and may consist of animals from several (5–10) leks. In fact our genetic data suggested that there was significant population differentiation between “winter flocks” in our study area, but also that males were differentiated among leks within winter flocks (Höglund *et al.* 1999).

We thus had to revise our thinking about lek evolution to incorporate these new findings. The new working hypothesis became this: by joining a lek where a relative is likely to reproduce, the attractiveness of the lek is raised and males unsuccessful in obtaining copulations may gain via inclusive fitness. This new idea incorporates the relatedness patterns we observed but also rests on the observation that females are more likely to mate in larger leks (*see also* Kruijt *et al.* 1972, Hovi *et al.* 1994, Lank & Smith 1994). So the implications for the study of the ecology and evolution of leks are that the new findings, if generally true among many lek species, will indeed affect the distribution models used to predict male settlement. There is also another attractive part of the kin selection idea. An old enigma in lek studies has been to understand why some males lek despite the fact they are never visited by females, or if visited not allowed to mate. With few exceptions (Lanctot *et al.* 1998, some years and leks in Fiske *et al.* 1994) most studies report a high and significant skew in male mating success within leks (Wiley 1991, Höglund & Alatalo 1995). If kin selection is operating the enigma is solved, such males gain through inclusive fitness.

Other species

Is it possible that the observed effects are particular to black grouse, or that our study population is somehow unique? Well, data are still scarce and few studies have been devoted to these issues. To date, I know two published accounts apart from the black grouse study. One by researchers within my own research group on white-bearded manakins (*Manacus manacus trinitatis*) and one from another research team on peacocks (*Pavo cristatus*). In peacocks Marion Petrie and co-workers using multi-locus fingerprinting found that band sharing was higher within than between leks, indicating that males were more related within than among leks (Petrie *et al.* 1999). This corroborates our findings (or *vice versa*), but the peacock study also provided even more intriguing detail. By using captive-reared brothers that had been kept apart since birth it was shown that these birds were more often lekking close to relatives than expected by chance. This suggests that some kind of kin-recognition mechanism (most likely self referent phenotype matching, Hauber & Sherman 2001) is at work and that male settlement is not simply a passive process produced by absence of natal dispersal, as might be the case in black grouse.

In white bearded manakins Lisa Shorey and co-workers showed that leks did not consist of only one kin group (Shorey *et al.* 2000). Instead in these birds, studied in rain forest habitat on Trinidad, both of the two studied leks consisted of two spatially separated kin clusters. This may affect the distribution of matings among males (Shorey 2002) but also makes it harder to detect the spatial pattern of population structure if detailed data on territorial positions are not available (J. Höglund & L. Shorey unpubl.). Thus, both this study and research conducted on the black grouse suggests that it may be misleading to use the lek as a unit of analysis when understanding kin structures within populations. In the case of black grouse, the winter flock may be a relevant and interesting level of organisation warranting further study. In the case of manakins it is intriguing why leks consist of several kin groups. Further study should be devoted to both costs and benefits of lekking with relatives. It is, for example, not at all clear if aggression is pre-

dicted to be reduced or elevated among relatives (Griffin & West 2002, Shorey 2002).

Conclusions

As stated above, it is too early to conclude whether or not kin selection will be a generally important factor in explaining the evolution of leks in many kinds of organisms. Even if kin effects turn out to be prevalent and widespread, it has been pointed out that kin structures may also be explained by direct benefits (Sæther 2002). Future research is needed to resolve this issue.

Finally, I would like to point out that it is interesting that kin selection theory has not until these rather late studies (reviewed here) been considered in lek studies. This is somewhat surprising since in studies of social insects, kin selection is and has been of central interest for decades (Crozier & Pamilo 1996). In social insect studies it may be argued that there is a slight move away from kin selection based explanations (e.g. Queller *et al.* 2000) and that direct selection explanations are presently often put forward. In the case of vertebrates/lekking birds, there is instead a move towards and a newborn fascination for kin selection arguments. You may wonder if this newborn fascination is unfounded? Perhaps as always, the truth may lie somewhere in between?

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