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COMMENTARY

On the evolution of hidden leks and the implications for reproductive and habitat selection behaviours

ROBERT J. FLETCHER JR* & CHRISTINE W. MILLER†
*Avian Science Center, Division of Biological Sciences, University of Montana
†Division of Biological Sciences, University of Montana

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> *...Wagner's 'hidden lek' hypothesis holds a great deal of promise for increasing our understanding of avian reproductive strategies...In addition, the puzzling clumped distributions of territories within homogeneous habitat can potentially be explained by this hypothesis* (**Ligon 1999**).

Habitat selection affects many aspects of individual fitness, which can have strong consequences for life-history strategies, species interactions, population dynamics and evolutionary trajectories (e.g. Danchin & Wagner 1997; Morris 2003). A potentially important link among habitat selection, sexual selection and mating systems was recently illustrated with the description of hidden leks by Wagner (1998). Hidden leks evolve in territorial species when female receptivity to extrapair copulations (EPCs) outside the social pair bond results in aggregations of territorial males (Wagner 1998). By drawing analogy from lekking behaviour in promiscuous species, Wagner provided novel insight into habitat selection behaviour. This hypothesis sheds new light on the evolution of conspecific attraction used in habitat selection (Stamps 1988), which has been documented experimentally in many taxa (e.g. Stamps 1988; Muller 1998; Ward & Schlossberg 2004). Conspecific attraction challenges assumptions of both habitat selection theory and metapopulation theory (Stamps 1988; Ray et al. 1991), but why attraction evolves remains largely unknown. The hidden lek hypothesis could help to explain attraction; however, robust criteria for detecting hidden leks and specific predictions of how hidden leks influence habitat selection behaviours have been obscure (Wagner 1998; Tarof et al. 2005). Here, we seek to refine and clarify predictions made from the hidden lek hypothesis, emphasizing how different models of hidden lek evolution can lead to different predictions for habitat selection and reproductive behaviours.

What is a Hidden Lek?

A hidden lek is loosely defined as an aggregation of territorial males that results from or is maintained by EPC behaviour (Danchin & Wagner 1997; Wagner 1998; cf. Tarof et al. 2005). The lek is hidden because territory sizes within an aggregation are typically larger than those in lekking species, resulting in a more cryptic (or larger-scale) aggregation than in traditional lekking species. Aggregations of males are thought to result from EPC behaviour when distances to extrapair mates are critical for access (Wagner 1998). In this context, aggregations typically refer to situations where observed dispersions of males show statistically aggregated patterns in space relative to random or hyperdispersed patterns (e.g. Sherry & Holmes 1985). We emphasize, however, that experimental documentation of males preferring to settle near conspecifics provides stronger inference for the individual-based processes that link habitat selection, aggregation and the potential for hidden leks.

To outline the requirements for hidden leks, we apply criteria for leks to species where females are receptive to EPCs. Bradbury (1981) invoked four criteria for leks (see also Höglund & Alatalo 1995): (1) absence of male parental care; (2) presence of an arena or lek where females come and most mating occurs; (3) display sites of males contain no significant resources; and (4) females have opportunities to select mates during arena visits. To form criteria for hidden leks, we need to determine how EPC behaviour changes lek criteria. Therefore, we propose the following criteria for hidden leks: (1) social monogamy or social polygyny, where females develop pair bonds with males who provide some form of parental care; (2) aggregations of territorial males, forming arenas where

Correspondence: R. J. Fletcher, Jr, Avian Science Center, Division of Biological Sciences, University of Montana, Missoula, MT 59812, U.S.A. (email: robert.fletcher@mso.umt.edu).

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EPCs occur; (3) females are receptive to EPCs and have opportunities to select extrapair mates; (4) no parental care from extrapair males; and (5) extrapair males do not monopolize resources required by females.

These criteria provide a framework for estimating the likelihood of hidden leks in nature. Criterion 1 is required for EPCs to be possible, and for some taxa, such as birds, social monogamy and social polygyny constitute the overwhelming majority of mating system structures (Griffith et al. 2002). It is often suggested that many species form aggregations of territorial males even where there are no noticeable gradients in habitat quality (Sherry & Holmes 1985; Stamps 1988; Greene et al. 1996; Muller 1998; Wagner 1998), consistent with criterion 2. Based on observed correlates of EPC and male phenotype, females often appear to select extrapair mates based on some measure of phenotypic quality (reviewed in Griffith et al. 2002), providing some support for criterion 3. Criterion 4 is thought to be common for many species engaging in EPCs (Birkhead & Møller 1992; Ligon 1999); indeed, if extrapair mates provide parental care, then the individuals have developed some sort of social pair bond and 'extrapair' may be inappropriate. Finally, criterion 5 is also considered common in many species engaging in EPCs (Birkhead & Møller 1992; Ligon 1999), although females in some species do procure additional resources from extrapair matings and these 'material benefits' may increase fitness (Gray 1997).

Based on this framework, we have good reason to conclude that hidden leks might be common in nature, particularly in birds. However, we stress that many of these criteria have only been addressed based on correlative observational studies (Westneat & Stewart 2003), making it difficult to infer causal pathways relevant to the hidden lek criteria, and most of these criteria have not been simultaneously addressed within a species or population. Furthermore, these criteria are necessary, but not sufficient, for understanding whether aggregations result from EPC behaviour, because other mechanisms independent of EPC behaviour could cause aggregations and conspecific attraction (reviewed in Stamps 1988). Rigorous testing of hidden leks will need not only to document the criteria above but also to confront the hidden lek hypothesis with other alternatives for aggregative behaviour. Tarof and colleagues (Tarof & Ratcliffe 2004; Tarof et al. 2005) provide a good example of both, examining characteristics of aggregative behaviour consistent with hidden leks and testing multiple alternative hypotheses to explain territorial aggregations in a socially monogamous songbird, the least flycatcher, *Empidonax minimus*. Not only does this species show characteristics consistent with hidden leks based on the criteria outlined above, but other alternatives to aggregation, such as predator dilution effects, cannot explain aggregative behaviours (Tarof & Ratcliffe 2004; Tarof et al. 2005; see also Hoi & Hoi-Leitner 1997, for an example with a colonial species).

Understanding the consequences of hidden leks for individuals and populations requires considering the circumstances that may have driven hidden lek evolution. Four common models for the evolution of leks can be applied to hidden leks, with each making distinct predictions regarding habitat selection behaviours and the relationship between EPCs and population density (Table 1). Below we couple information on habitat selection and EPC behaviours to allow careful differentiation of these models (Table 1), which can provide insight into the relationships between reproductive behaviours, sexual selection and habitat selection.

Models of Hidden Lek Evolution

The hotshot model

In the hotshot model of lek evolution, certain 'hotshot' males are preferred by females (either because of dominance or other phenotypic traits; Beehler & Foster 1988; Höglund & Alatalo 1995), such that the hotshots obtain a disproportionate number of matings, and subordinates aggregate near hotshots to increase mating opportunities. This model can be readily extended to hidden lek evolution if females choose hotshots for EPCs but develop social pair bonds with subordinates to gain assistance with parental care, since the hotshot will develop social pair bonds only with a limited number of females (see Wagner 1998). In hidden leks, female preference for hotshots results in two possible scenarios for settlement: (1) females settle near hotshots and subordinates follow, or (2) subordinates settle near hotshots and females follow. These subordinate males will typically lose paternity to hotshots, but they will increase their likelihood of social pairing success, which may have net fitness benefits. Necessary social pair bonds between females and their social mates would discourage hotshot males from deserting the aggregation, thus creating a situation with higher stability than in hotshot models of classical leks (see Höglund & Alatalo 1995).

In the hotshot model of hidden leks, conspecific attraction should occur for subordinate, rather than dominant, males (e.g. Ward & Schlossberg 2004). Alternatively, hotshots could aggregate around subordinate males to parasitize EPCs; however, this situation is generally unlikely because subordinates typically settle in areas after dominants in most systems (e.g. Wagner 1998; Greene et al. 2000). While Wagner (1998) argued that in the hotshot model females might not benefit from male aggregation and could potentially suffer some fitness costs through courtship disruptions, females may reap an overall benefit from aggregations because of their increased access to the extrapair hotshot. The hotshot model predicts EPCs should be biased towards hotshots (Fig. 1), but EPC rate does not necessarily increase with aggregation size. Instead, EPC rate should increase with an increasing number of hotshots in the aggregation (Table 1). Thus, the hotshot model makes distinct predictions about which members of a population should show attraction and how EPCs should occur (Table 1). An intriguing example that supports some elements of the hotshot model comes from lazuli buntings, *Passerina amoena*. Lazuli buntings are migratory songbirds that may form territorial clusters during the breeding season (Greene et al. 1996). Greene et al. (2000) documented that subordinate males that aggregated around dominant males had higher social pairing success and fitness relative to other subordinate males,

Table 1. Predictions for different models of hidden lek evolution

	Predictions for*					
	Habitat selection behaviours			Reproductive behaviours		
Hidden lek model	Do all males show conspecific attraction and aggregate?	Female spatial behaviours	Other	Does EPC increase (per capita) with density or aggregation size?	Is EPC biased towards certain phenotypes?	Other
Hotshot	No	Preferentially settle near hotshots	Dominant male is centralized	No prediction	Yes	EPCs increase with increasing number of hotshots
Female preference	Yes	Preferentially settle in large aggregations		Yes	No prediction	
Hotspot	Yes	Large overlapping home ranges relative to male territory size or well-defined travel routes, causing areas of high encounter rates	Male aggregations decline with increasing female density	No	No prediction	Areas of high EPC rates occur
Kin selection	No, subordinates only	Preferentially settle in large aggregations	Male natal philopatry Males preferentially settle near relatives	Yes	Yes	Subordinates gain inclusive fitness benefits according to Hamilton's rule

*Compiled or modified from: Wagner (1993), Höglund & Alatalo (1995), Kokko & Lindström (1996), Wagner (1998), Tarof et al. (2005).

even though they experienced cuckoldry from dominant males. However, the process of female habitat selection behaviour in this species was not thoroughly examined, which limits inference on whether the hotshot model was operative in this population.

Female preference model

In the female preference model of lek evolution, females prefer aggregations of males and tend to ignore or bypass males that have established solitary territories (Bradbury 1981). Females benefit from male aggregation for two possible reasons: (1) they can appraise males in groups or arenas to estimate relative male quality (Wagner 1998) and (2) male quality can increase on average with increasing aggregation size (Höglund & Alatalo 1995). This model can also be extended to hidden lek evolution if females prefer aggregations for increased EPC opportunities (see Wagner 1998). In this case, females may benefit from clustering, and both pairing success and EPCs should increase

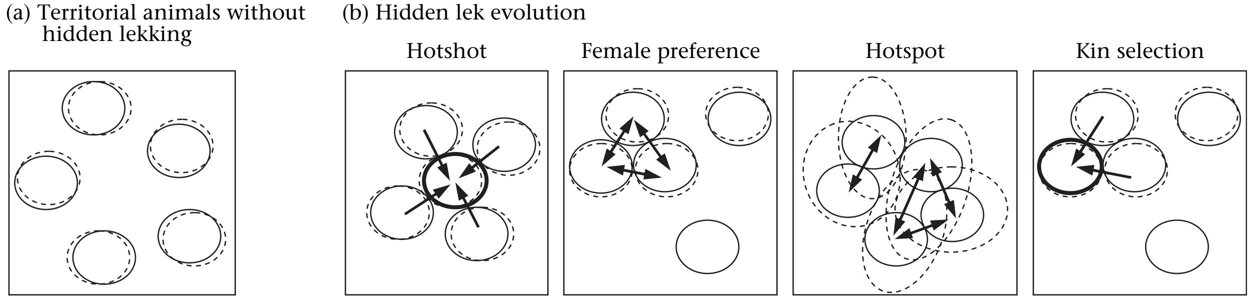

Figure 1. Diagrams of the spatial distribution of male territories (solid circles) and female home ranges (dashed circles) for (a) territorial animals without hidden lekking and (b) different models of hidden lek evolution. In the hotshot model, subordinates aggregate around hotshots (thick circle) to increase their chances of mating success, but subordinates loose paternity to hotshots because females bias extrapair copulations (EPCs; arrows) towards hotshots. In the female preference model, females prefer aggregations of males for EPC opportunities. EPCs increase (per capita) with aggregation size, but there are no explicit predictions for EPC bias based on male phenotype (double-sided arrows). In the hotspot model, areas of high female activity occur based on large overlapping home ranges relative to male territories (shown) or based on well-defined travel routes. Aggregations form by males settling in areas of high female encounter rates. EPCs do not increase with aggregation size and there are no explicit predictions for EPC bias. The kin selection model shares some similarities with the female preference and hotshot models, except it invokes inclusive fitness to explain aggregation of subordinates. Dominant males benefit from the presence of related subordinates, based on biases in EPCs.

(per capita) as a function of aggregation size or density (e.g. Tarof et al. 2005; Fig. 1). All types of males are expected to show attraction in this model (Table 1).

The hotspot model

The hotspot model of lek evolution developed by Bradbury et al. (1986) hypothesized that males aggregate near locations of high female activity, which could occur from female use of rare resources (such as foraging hotspots), from female home range overlap, or from well-defined travel routes (see also Westcott 1997). Thus, the clustering of males is based on the clustering of female activity, which may or may not be based on clustered resources (Höglund & Alatalo 1995; Westcott 1997).

For hidden leks to occur from hotspots, females need only to have large home ranges relative to male territory size, or they need to have well-defined travel routes (Bradbury et al. 1986; Westcott 1997). Large female home ranges or well-defined travel routes can increase overlap among female activity, resulting in areas of high female encounter rates. Males situating territories near these hotspots could accrue a higher likelihood of pairing success and EPCs, assuming females are receptive to EPCs (Fig. 1). For species where males settle before females, males may use a variety of cues for settling in areas of anticipated female distribution (see Bradbury et al. 1986). While males could suffer increased likelihood of cuckoldry in colonies or aggregations (Wagner 1993), increased likelihood of pairing success may outweigh the potential costs of cuckoldry (e.g. Greene et al. 2000). Thus, for this model to apply to hidden leks, males aggregate to increase pairing success and EPCs are merely a by-product of the aggregation; once aggregated, it behooves males to engage in EPCs (Trivers 1972; Ligon 1999). This model predicts that all males should settle near hotspots (when available) and that EPC rate does not increase on a per capita basis with aggregation size. The hotspot model does not make explicit predictions for EPC bias based on phenotype; however, if males settle in a staggered manner, earlier settlers may receive more EPCs by settling in ‘hotter’ hotspots. Another prediction that arises from this model is that EPCs will occur during female forays to hotspot areas (Table 1), resulting in areas of high EPC rates.

The kin selection model

Kin selection has also been recently invoked as a model for the evolution of leks (Kokko & Linström 1996). Kin selection and inclusive fitness may help to explain why subordinate males will join leks, even when the likelihood of securing copulations is virtually nonexistent. For kin selection to operate in leks, the following must generally occur: (1) females must prefer aggregations such that the dominant male receives a benefit from subordinate male presence, (2) lek members must be related, (3) subordinate males have a low mating probability; thus Hamilton’s rule ($rB - C > 0$; where r is the coefficient of relatedness to dominant male, B is the benefits from lekking in the absence of mating and C is the costs of joining a lek) should be met for subordinates to join a lek (Kokko & Linström 1996; Sæther 2002) and (4) subordinate males must not receive other direct benefits that outweigh indirect benefits (Sæther 2002). While this model has been applied to animals that show high male natal philopatry (Kokko & Linström 1996), kin recognition or variation in female preferences for certain phenotypes could drive lek behaviour (Petrie et al. 1999; Sæther 2002). The kin selection model shares some similarities with the female preference model in that females prefer aggregations of males (Kokko & Linström 1996). However, this model seeks to explain male aggregation of subordinates by invoking inclusive fitness.

Kin selection could cause hidden leks, particularly for taxa, such as birds, that have male-biased natal philopatry (Greenwood & Harvey 1982). However, this might be unlikely under most circumstances; the potential for indirect inclusive benefits is relatively low since EPCs often make up less of the total realized success than do within-pair copulations (e.g. Webster et al. 1995; Freeman-Gallant et al. 2005). Predictions for habitat selection behaviour of females are similar to the female preference model; for males, predictions include male-biased natal philopatry and subordinates settling preferentially near relatives (Fig. 1, Table 1). Predictions for reproductive behaviours include increased EPCs with aggregation size, biases in EPC towards the dominant male, resulting in an EPC-related benefit from subordinate male presence, and subordinates gaining inclusive fitness benefits from related, dominant males (Fig. 1, Table 1).

Conclusions

The discovery that extrapair copulations are common in many socially monogamous species, particularly birds, has revolutionized our understanding of mating systems, and the hidden lek hypothesis offers much promise in understanding links between extrapair copulations, dispersal and species distributions (Danchin & Wagner 1997; Wagner 1998; Ligon 1999). Given the criteria we have developed for hidden leks, it appears that hidden leks could be common. Few studies to date, however, have documented all criteria for hidden leks within a population while comparing this hypothesis with other alternatives for aggregative behaviour. Furthermore, different models of hidden lek evolution make different predictions for both reproductive and habitat selection behaviours, so testing these alternative models will prove critical for understanding and predicting when hidden leks should occur. While these models could operate alone or in concert, information on male aggregative behaviours and EPC frequency as a function of aggregation size can help to decipher which models of hidden lek evolution are operative (Table 1). By linking habitat selection with mating system structure, we will be one step closer to understanding the evolution of aggregative behaviours, predicting the generality of conspecific attraction and interpreting the influence of EPCs on reproductive behaviours in territorial species.

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