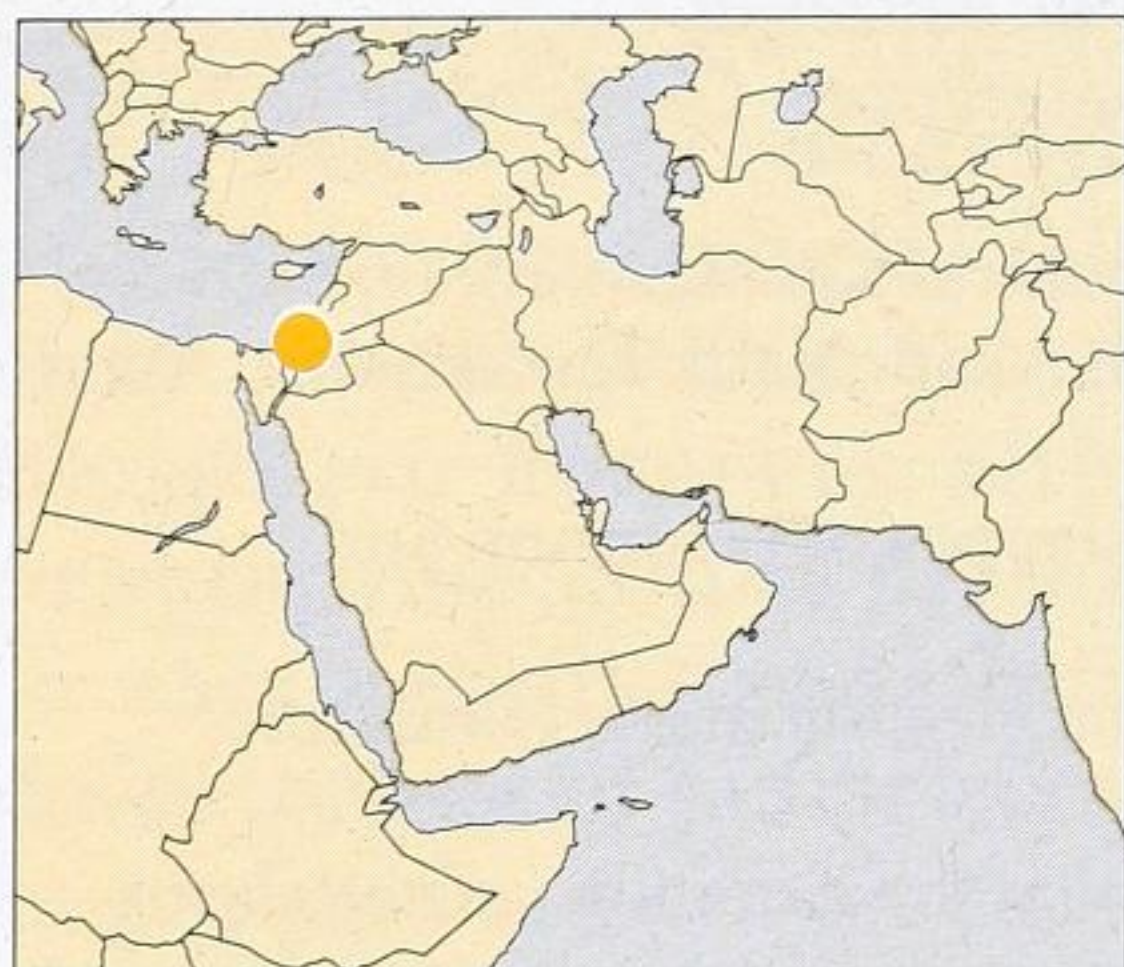


Lek-like behaviour by Chukar *Alectoris chukar*, a socially monogamous partridge

SALIT KARK



Lekking behaviour is known in various socially polygamous bird species, including phasianids. Lek-like behavior in socially monogamous birds has recently been reported in several colonial species. These cases support the Hidden Lek Hypothesis, which proposes that males cluster breeding territories in response to the pursuit of multiple copulations by females. Here, I report lek-like behaviour in Chukar *Alectoris chukar* in Israel. This provides primary evidence that lek-like behaviour can occur in a non-colonial, socially monogamous species. Further studies of the breeding behaviour of socially monogamous phasianid species may produce new insights into lekking behaviour, its ecology and evolution.

INTRODUCTION

THE SOCIAL BEHAVIOUR OF LEKKING, which is described as an aggregation of displaying males visited by females primarily for copulation (Höglund & Alatalo 1995), is known in various animal groups, including birds, mammals, fish, amphibians and insects. Definitions of lek vary (see Höglund & Alatalo 1995). Bradbury (1981) presented four criteria for a 'classical' lek: male paternal care is not involved; an arena is used in an area not normally used for other activities such as feeding and roosting; a display site, which does not contain significant resources except for males, is used; and females have an opportunity to select males. While the first and last criteria are often debated, it is usually agreed that females visit leks solely to assess males and to mate (Westcott 1994). Males in a lek are more aggregated at the display habitat than would be expected by random distribution (Höglund & Alatalo 1995).

Lekking behavior has been widely studied both theoretically and empirically in many socially polygamous bird species (Höglund & Alatalo 1995, Loffredo & Borgia 1986), but has rarely been observed in socially monogamous taxa (Wagner 1997). Although sexual selection is considered stronger in polygamous species (Darwin 1874), it is also expected to occur in socially monogamous forms (Møller 1994, Trivers 1972). This prediction is especially relevant in relation to increasing evidence for extra-pair copulations (EPCs) in many avian species (Petrie & Kempenaers 1998), which suggests that social monogamy does not always reflect mating patterns. A recent theory, the Hidden Lek Hypothesis (Wagner 1997), proposes that males cluster breeding territories in response to the pursuit of multiple copulations by females. Lek-like behaviour in socially monogamous birds has only recently been reported. Wagner (1992, 1993) found that the socially monogamous Razorbill *Alca torda* pursues EPCs in lek-like mating arenas within the vicinity of the colony, but outside the breeding territory. These aggregations function as leks, exhibiting all of the criteria given above (Wagner 1997). The Hidden Lek Hypothesis is supported in two other birds, Purple Martin *Progne subis* (Morton *et al.* 1990, Wagner *et al.* 1996) and Bearded Tit *Panurus biarmicus* (Hoi & Hoi-Leitner 1997), which display lekking behaviour inside their colony. Components of their breeding system suggest that a lek may be 'hidden' within a colony (Wagner 1997). In all these cases lekking behaviour was described in species and populations with colonial mating systems.

Among birds, leks are common in various socially polygamous phasianid species, including the two best known, Sage Grouse *Centrocercus urophasianus* (Gibson 1992) and Black Grouse *Tetrao tetrix* (Höglund & Alatalo 1995). Here, I report the first evidence for lek-like behaviour in Chukar *Alectoris chukar*, a non-colonial, socially monogamous phasianid (Alkon 1974, Shirihai 1996). The behaviour occurred outside the breeding territory of at least some of the participating individuals within an open area in Jerusalem, Israel. To my knowledge, such behaviour has not been previously reported in a non-colonial monogamous species.

STUDY AREA

Chukar inhabits open and semi-open areas of Eurasia (Alkon 1974, Shirihai 1996). In Jerusalem, rapid urbanisation in recent years has resulted in the development of many formerly open areas within the city limits. As a result, Chukar distribution in the city has become very patchy (pers. obs.), but a population persists around the Hebrew University Campus of Givat Ram, the Israel Museum and Monastery of the Cross, in open fields, olive groves and the University Botanical Gardens. This region of the city is open and relatively continuous, allowing several Chukar coveys to persist. West of the Israel Museum, a natural field (c. 500 metres x 100 metres) is maintained, with native Mediterranean garrigue vegetation.

In this area, over three years (1995–8) I studied a Chukar covey, which varied in size from seven to nine adults and was continuously present. Members of the covey apparently failed to successfully reproduce, though I found evidence for several nesting attempts (a deserted nest of 14 eggs in May 1995 and a brood, c. 1 week old, which later disappeared). No other coveys were regularly observed in this field during the period, though coveys were found in adjacent areas. These observations accord with studies of the species' social structure suggesting that in the non-breeding season (September–February inclusive in Mediterranean Israel; Alkon 1974) Chukar forms stable coveys with relatively fixed home ranges (Alkon 1974). In the breeding season, coveys disband into pairs, each establishing a nest site and maintaining a breeding territory (Shirihai 1996). In Mediterranean Israel pair formation and copulation usually commence in March (Alkon 1974), and egg-laying has been observed in March–August (Shirihai 1996).

LEK-LIKE BEHAVIOUR IN CHUKAR

At c. 10.00 on 4 May 1996 (during the breeding season), I observed lek-like behaviour by Chukar in the field described above. Early May marks the beginning of the dry season; the behaviour I observed occurred during a climatic event known as Hamsin, which is characterised by very hot, dry and windy weather. The lek-like behaviour occurred within a well-defined central area, located on a stone-built terrace of four large steps, each approximately one metre high and 20 metres long, comprising rectangular blocks c. 1–2 metres long and two metres wide. The location did not possess known significant resources such as nest sites, food or water. The behaviour was observed within a rectangular central area, c. 1 metre x 1.5 metres, and occurred repeatedly over a period of >15 minutes as follows: while several individuals were perched on adjacent steps, one would jump from an upper step at the south-east corner into the lower central area, where another individual was waiting. The two immediately clashed, flapping their wings and jumping into the air simultaneously, while facing each other. Those individuals in the central area would spin in the air to a height of c. 1 metre while clapping their wings, repeating this several times until one left the central area (usually at the upper north-east corner). The other remained while another individual entered the area from the south-east top corner and the next

confrontation commenced. This behaviour occurred repeatedly, different individuals entering and exiting the arena. In several cases two pairs of combatants were observed clashing simultaneously within the same central area. I did not notice mating following the display at the arena.

No individuals in the area had been individually marked. Except size differences (male larger) and spurs (presence typical of adult males), male and female Chukar are not easily distinguishable (their coloration or feather patterns being similar). It was therefore difficult to determine the sexes reliably at a distance of c. 20 metres. Nevertheless, I managed to detect spurs on several individuals as they entered the central clashing area, thus confirming the participation of males in this behaviour. It was difficult to accurately estimate the total number of individuals present because they constantly changed positions around the central area. However, I observed at least 11 individuals among the total of c. 25 gathered within a few metres of the central area. Throughout the 15 minutes the birds uttered very high, sharp calls. Similar calls were defined by Alkon (1974) as aggressive-behaviour related calls.

Twice I observed aggregations of more than nine individuals in the study area, and in both cases these were characterised by intense activity and loud calls. The first (in September 1996) involved at least 17 individuals and the second (in January 1998) at least 14 birds. Both were in the non-breeding season and in neither did I observe grouping around a central area or mid-air clashes. All three aggregations (including the behaviour detailed above) involved more individuals than in the local covey.

DISCUSSION

While aggregations of Chukar are known from elsewhere in Israel, none has been related to breeding behaviour. Alkon (1974) observed several cases of social aggregations of 40 to over 100 birds, especially in late summer when broods were present, but did not relate these to breeding behaviour. Aggregations of several dozens and up to c. 150 birds occur in the desert during the non-breeding season and near food- and water-rich resource areas (pers. obs.). Shirihi (1996) also reports foraging-related Chukar aggregations numbering dozens of birds.

Alkon (1974) observed clashing behaviour among single Chukar males in north Israel. He related this to an intense form of mutual aggression, termed 'frontal mid-air clashes'. He described this behaviour as one in which 'the two combatants faced and then jumped towards each other to a height of 1.0–1.5 metres while flapping their wings and striking with their legs' He regarded this as an encounter between highly motivated males of equal status and related it to aggressive behaviour, and differing from my observation in that it was not accompanied by aggregation around a central area. The timing of the behaviour also differed, as it occurred during the peak rather than at the end of the breeding season in the Mediterranean region (Alkon 1974). Based on the first criterion presented in Höglund & Alatalo (1995), Chukar would not be considered a classical lek species. Though males usually leave their mates shortly after egg-laying, male paternal care may take the form of nest guarding (Alkon 1974), although paternal care, according to Höglund & Alatalo (1995), is not necessary for defining a lek. The remaining three criteria described for a lek, an arena within an area, which is not normally used for other activities, a display site that does not contain resources except for males and an opportunity for females to select mates, may well apply.

Hypothetical explanations for the unusual behaviour observed include the following. The patchy environment in which the species occurs in Jerusalem and the resulting

small size of local populations may enhance the need to gather with individuals from neighbouring coveys to form pairs and rebuild coveys. Aggregating within a central area and the mid-air clash confrontations may act as means to evaluate the quality of individuals from several coveys for mating or for creating new coveys. The behaviour occurred within the peak breeding season and may thus be related to nesting, covey building or evaluation of mates for future breeding seasons. Aggregation may also function as a meeting arena for first mating or for re-mating of males and females whose first breeding attempt failed, and finally Chukar may aggregate in one area to select mates but may copulate elsewhere.

Alkon (1974) demonstrated that re-nesting during the breeding season was common in Chukar in the Lower Eastern Galilee of Israel, due to the failure of the majority of initial nesting attempts. The behaviour I observed may also serve as a means for post-fertile females to appraise males through EPC, in order to test their potential as mates or extra-pair fertilisers in the next breeding season, as suggested by Wagner (1992) for Razorbill. Females of the latter species incite competition in the form of combats between males, in order to evaluate them as future mates (Wagner 1992). It appears that EPC is unstudied in Chukar and may be unknown. Because, at least in some cases, males rebuild new coveys following the breeding season (Alkon 1974, pers. comm.), the lek-like behaviour, which was not followed by mating, may serve as a means of status determination among males for the purpose of covey creation, although this is speculation. Westcott (1997) demonstrated that in Ochre-bellied Flycatcher *Mionectes oleagineus* male–male interactions might be important in determining lek structure. Further detailed studies of the behaviour of Chukar and other socially monogamous phasianid species may produce new insights into lekking behaviour, its evolution and ecology.

CLOSING REMARKS

Intensive human-related activity, including habitat fragmentation and game hunting are impacting Chukar in Israel, and appear to be modifying patterns of gene flow and the genetic structure of local populations (Kark *et al.* 1999). Loss of connectivity between Chukar populations may influence covey aggregation patterns and affect social behaviour and the genetic structure of populations. Chukar is an open-country species capable of persisting at the fringes of human-modified areas until disturbance levels become high. It may therefore be a good candidate for monitoring and evaluating the effects of reduced open areas and their wildlife populations, which are rapidly disappearing throughout Israel.

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