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Genetic Structuring and the Evolution  
of Lekking Behaviour in the  
White-bearded Manakin, *Manacus  
manacus*

BY

LISA SHOREY



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## Abstract

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Genetic structuring is common in natural populations. It is important to identify and consider population structure when studying evolutionary processes. Recently, the discovery of genetic structuring in some lekking bird species has opened up new perspectives on our understanding of the evolution of lek mating systems.

This thesis uses molecular data to identify patterns of broad and fine scale genetic structuring in the lekking white-bearded manakin *Manacus manacus*. Additionally, data on male mating success, female visiting patterns and behavioural, morphological and territorial characteristics of individual males are used to identify variables that may influence the distribution of matings in this species.

Analysis of genetic divergence within the genus *Manacus* revealed genetic sub-structuring and limited gene flow between species/subspecies. There was no significant isolation by distance relationship. Factors such as physical barriers to gene flow may play a role in shaping the genetic structure of the bearded manakin genus.

White-bearded manakin leks on Trinidad were composed of groups of related males. More than one such kin group existed on each lek. That related males gather in groups suggests that genetic structuring is not simply a consequence of limited dispersal. Active choices must take place by both residential and newly arrived birds.

Female visits to, and matings with, males were non-random. Centrality of male display court was the only measured variable that consistently correlated with male mating success. More aggressive displays were made as the distance between courts decreased. There was no significant relationship between the number of aggressive displays made between males and relatedness levels. Males with high mating success spent more time in aggressive behaviours.

In conclusion, white-bearded manakin lek formation and display court acquisition is likely to be influenced by genetic relatedness levels and male-male interactions. Centrality of court seemed important in mating success and may be an indicator of male dominance. However, a variety of other factors may also influence mating success and may be variable over time.

*Key words:* Lek evolution, *Manacus manacus*, white-bearded manakin, genetic relatedness, mating success, male characteristics, behaviour

Lisa Shorey, Evolutionary Biology Centre, Department of Population Biology, Uppsala University, Norbyvägen 18D, SE-752 36 Uppsala, Sweden ([Lisa.Shorey@ebc.uu.se](mailto:Lisa.Shorey@ebc.uu.se))

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Some regard the tropics as an equatorial Dante's Inferno, the so-called Green Hell. The rainforest: abominably hot, oppressively humid, crawling with vile scorpions, immense, hairy, ugly tarantulas, lethal, concealed snakes, marauding, biting, stinging, and generally irritating insects, not to mention countless legions of external and internal parasites awaiting to devour you from without and within. Well, calm down, don't get excited...

Kricher 1997

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This thesis is based on the following six papers, which will be referred to in the text by their Roman numerals **I-VI**

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- I** Höglund J and Shorey L. Genetic divergence in the superspecies *Manacus*. Submitted manuscript
- II** Shorey L, Piertney S, Stone J and Höglund J. Fine scale genetic structuring in *Manacus manacus*. *Nature* **408**: 352-353
- III** Höglund J and Shorey L. Local genetic structure in a white-bearded manakin (*Manacus manacus*) population. Submitted manuscript
- IV** Shorey L. Mating success on white-bearded manakin (*Manacus manacus*) leks: male characteristics and relatedness. Accepted for publication in *Behavioral Ecology and Sociobiology*
- V** Shorey L. Female visiting patterns in the white-bearded manakin (*Manacus manacus*): potential for mate-choice copying. Manuscript
- VI** Piertney S, Shorey L and Höglund J. Characterisation of microsatellite DNA markers in the white-bearded manakin (*Manacus manacus*). Accepted for publication in *Molecular Ecology Notes*

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Cover painting by: Dave Showler, Brasso Seco, 2000

## **INTRODUCTION**

The presence of genetic structuring in any population or subpopulation is an important factor influencing many aspects of research. Indeed, population structuring appears to be a common phenomenon of most, if not all, species and this may be due to a variety of non-mutually exclusive agents such as environmental barriers, historical processes and life histories (for examples see Balloux and Lugon-Moulin, 2002). Exchange of genes between populations will be influenced by factors such as the geographic distance between them (isolation by distance) and by the dispersal abilities of the organism (gene flow). Speciation processes will be positively or negatively influenced by such factors.

Populations are often composed of more than just randomly mating subpopulations, with many organisms forming social groups with distinct patterns of mating and dispersal (Sugg et al., 1996). For example, non-random mating is a common phenomenon (Thornhill, 1993), many organisms exhibit social organisations that give some individuals an advantage in obtaining mates (Emlen and Oring, 1977; Thornhill and Alcock, 1983) and in many species there is sex-biased dispersal (Greenwood, 1980; Dobson, 1982). The relatively recent development of molecular techniques (in particular microsatellites) to distinguish genetic differences between individuals or groups of individuals has opened up a whole new perspective in our understanding of evolutionary processes and in the evolution of mating systems. Through the combination of genetic and behavioural data and the consideration of both social and population structure we can get a much better insight into past, present and future genetic variation (Sugg et al., 1996).

In this thesis the importance of genetic structuring is discussed in relation to the formation of lek mating systems. Leks are arenas where males aggregate and display in order to attract females for mating (Höglund and Alatalo, 1995). High variance in male mating success is a typical feature of lekking systems and has been observed in many species (for reviews, see

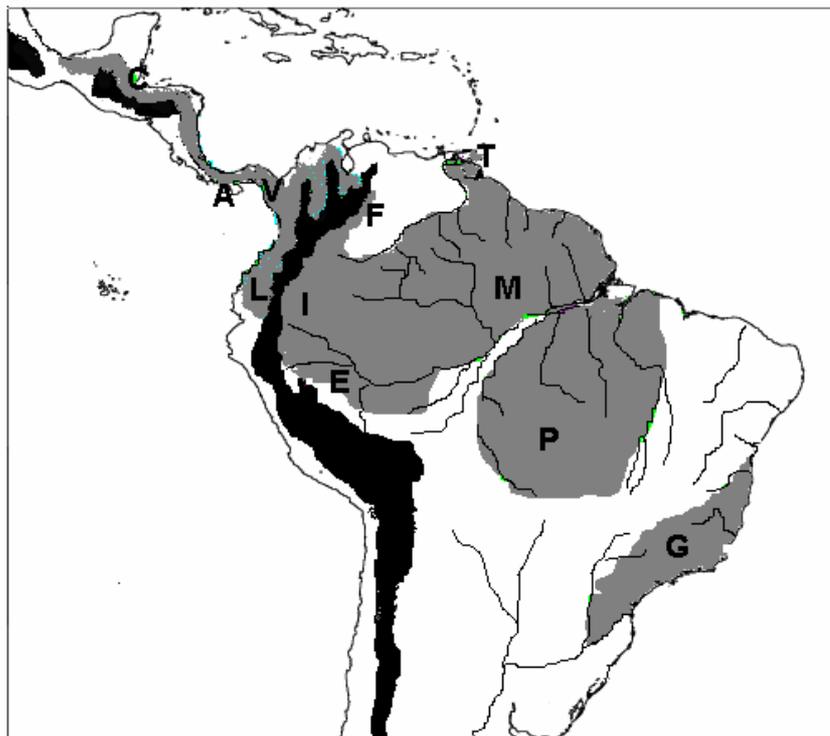
Bradbury et al., 1985; Wiley, 1991; Höglund and Alatalo, 1995). Traditionally, direct fitness benefits have been considered to be the primary force driving the evolution of lekking behaviour. However, recently it has become apparent that leks of some bird species show kin structuring (Kokko and Lindström, 1996; Höglund et al., 1999; Petrie et al., 1999; Shorey et al., 2000). This structuring allows the potential for indirect mechanisms such as kin selection (Hamilton, 1964) to operate. Such structuring may be influential on male-male social interactions that may influence territory acquisition and ultimately influence female mate choice.

Paper **I** takes a broad scale view of the genus *Manacus* found in Central and South America, in an attempt to identify the amount of divergence between previously classified species/subspecies using molecular data. All other papers concentrate on the subspecies *Manacus manacus trinitatis* found on the island of Trinidad. Papers **II** and **III** investigate genetic structure in the study population both within leks and between leks, highlighting the importance of identifying the correct scale of population genetic analysis and of combining population genetics with behavioural observation. Papers **IV** and **V** focus on factors that may influence male mating success and female mate choice. Paper **VI** describes characterisation of the microsatellite DNA markers used in the study.

### **The Study Species**

The bearded manakins (genus *Manacus*) are frugivorous, lekking, neotropical passerines belonging to the family Pipridae that are commonly found in mid-tropical woodlands, lower growth of shrubby or secondary woodland and forest borders (Ridgely and Tudor, 1994). Male nuptial plumage colour varies with geographic location and has been the basis for assigning either species or subspecies status to populations throughout the range. This geographic variation involves colouration and width of the collar, colouration of the cheek,

belly and back. Bearded manakins are highly sexually dimorphic, with females having inconspicuous green plumage. Juvenile males have delayed plumage maturation and have female plumage characteristics until their second year (Snow, 1962). They occur from southern Mexico throughout Central America and on both sides of the Andes as far south as southern Ecuador/northern Peru and the Amazon basin. They are absent from much of Venezuela (east of the Sierra Occidental and west and north of the Orinoco). A disjoint range is found in coastal SE Brazil (Figure 1).



**Figure 1** Map of the bearded manakin distribution (grey) depicting major rivers and mountain ranges (black).

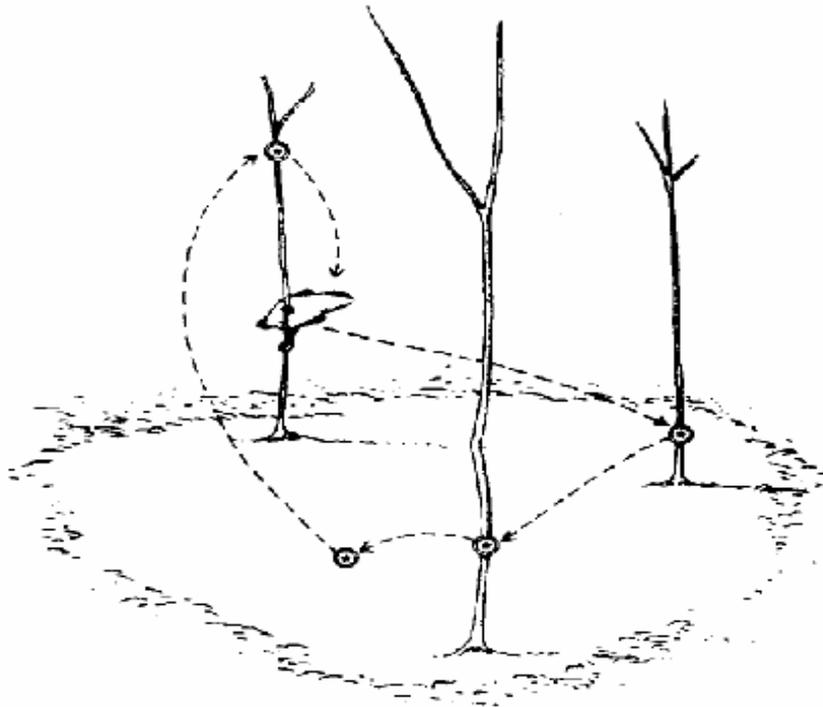
C=*Manacus candei* - white-collared manakin, V= *vitellinus* - golden-collared manakin, A= *aurantiacus* - orange-collared manakin, M= *manacus*, F= *flaveolus*, E= *expectatus*, G= *gutterosus*, L= *leucochlamys*, I= *interior*, P= *purus*, T= *trinitatis* - white-bearded manakins

In the Birds of the World Vol. 8 (1979) all bearded manakins are treated as conspecific (*M. manacus*). In the 1983 AOU checklist *vitellinus*, *aurantiacus* and *candei* are treated as separate species whereas all other populations are described as subspecies of *M. manacus*

White-bearded manakins have a concentrated lek system (Prum, 1994), where males congregate and perform displays to attract females for mating (Snow, 1962). On Trinidad, leks may consist of between 6-60 males (Lill, 1974) and are situated on or on the side of ridges, usually not more than 100 metres above a stream (Snow, 1962; pers. obs.). Females nest along the stream edges (Snow, 1962). The structure of the lower vegetation is crucial for the formation of a lek as the white-bearded manakin depends on small, upright saplings for its courtship display (Snow, 1962). The display takes place on a territory or 'court' that each resident male holds - an area of forest floor that he has cleared of leaves. Courts may be very close to each other or even share boundaries (pers.obs.). Each white-bearded manakin court must contain at least two emergent saplings, between which an acrobatic display is performed (Fig.2). The display is used to attract females for mating. Males actively display on the lek for the majority of the year with most nesting attempts by females being made between March and July. Once established, leks may persist for many years as long as vegetation remains unchanged and males may hold the same court from year to year (Snow, 1962). Males may live up to 15 years (Snow, 1962; Lill, 1974).

*The display*

The male white-bearded manakin produces snapping and cracking sounds made by modified (stiffened) primary wing feathers (Lowe, 1942). The mechanical sounds made by the male have been termed snapping, rolled snapping, grunt jumping and fanning (Snow, 1962). In the courtship display these sounds are combined with rapid flight between the display saplings and protrusion of the beard (Figure 2).



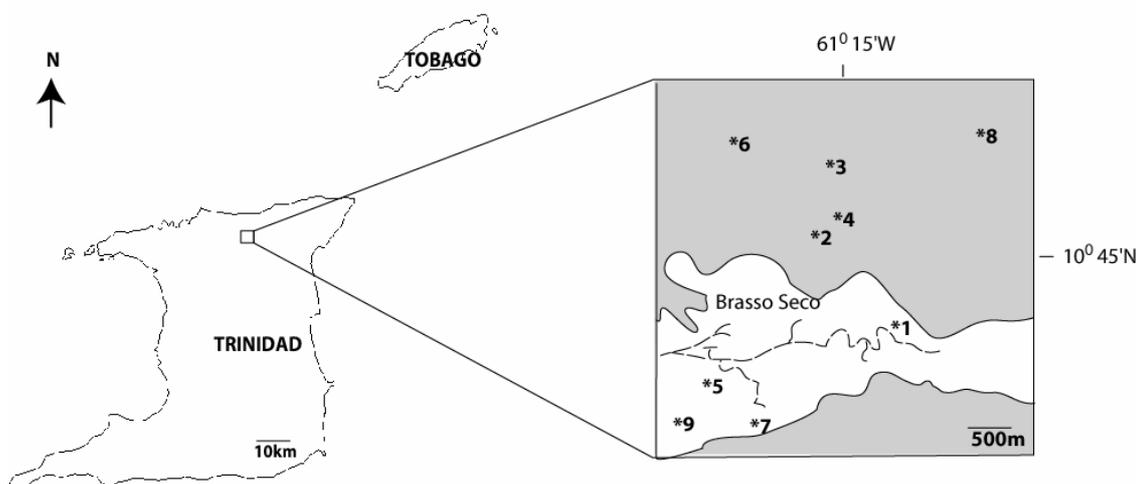
**Figure 2** A male manakin on his display court. The male jumps between the saplings whilst performing an acrobatic display. H. Sick 1967

## **METHODS**

### **Field methods**

Leks were studied in a 16 km<sup>2</sup> area of Paria, Northern Trinidad (site centre at 10°45'N, 61°15'W). In April/ March 1998 male, female and juvenile birds were captured on nine focal leks using mist nets. Leks were situated in lowland seasonal forest and cultivated areas (Figure 3). In total 250 birds were captured and each was given both a metal ring with a unique number and a unique combination of colour rings for individual identification in the field.

Approximately 4 µl of blood was taken from the wing vein and was stored in EDTA buffer. Morphological measurements of head, bill, wing and tarsus length were taken (Paper IV). Birds were then released to facilitate behavioural observations (Papers IV and V).



**Figure 3** Map of the study area surrounding Brasso Seco village, Trinidad showing the location of focal leks (1-9). Shaded area = forest vegetation, unshaded area = cultivated vegetation, dashed line = road

## **Collection of genetic data**

### *Sampling*

For analysis of broad scale genetic structuring in the superspecies *Manacus* (Paper I) we used a collection of 109 bearded manakin skins housed at the Natural History Museum in Stockholm, Sweden. Using sterile scalpel blades, a small piece of skin was removed from the footpad of each bird and stored in EDTA buffer. In addition we used blood samples from 20 birds captured at the study population on Trinidad.

In analyses of local and fine scale genetic data (Papers II, III and IV) we used blood samples from birds captured at the study site on Trinidad. Blood was taken from the wing vein and stored in EDTA buffer.

### *DNA extraction*

DNA was extracted from blood samples using standard phenol-chloroform procedures (Maniatis et al., 1982) and from foot scrapes using a DNeasy Tissue Kit, (Qiagen) following the manufacturer's protocol. Extracted DNA was dissolved in water and stored at  $-20^{\circ}\text{C}$ .

### *Genotyping*

Microsatellite variation was determined using 4-8 loci specifically cloned in the bearded manakin (Paper VI). DNA fragments were amplified using polymerase chain reaction (PCR, Saiki et al., 1985). PCR products were separated using polyacrylamide electrophoresis for 60-90 minutes at 75 W in 6% polyacrylamide gel. Products were visualised using silver staining. Negative controls (containing all reaction components except template DNA) were run alongside samples. To distinguish between female and juvenile male birds, primers P8 and P2 (Griffiths et al., 1998) were used. Procedures for DNA amplification were as described in Griffiths et al., 1998. These primers are

located on the sex chromosomes and since, in birds, females are the heterogametic sex (ZW), the fragment amplified on the W differs in length from the fragment on Z in almost all bird species studied (Griffiths and Orr, 1999). Electrophoresis and visualisation were carried out as above.

None of the loci used were in linkage disequilibria and allele frequencies did not deviate from Hardy Weinberg expectations.

### **Analysis of genetic data (Papers I-IV)**

#### *Broad scale genetic structure (Paper I)*

Bottleneck (Cornuet and Luikart, 1996) was used to check for evidence of recent population size bottlenecks where we had sufficient data. PHYLIP 3.5c (Felsenstein, 1993) was used to perform bootstrap analyses (n=1000) and to construct neighbour joining phenograms. GENEPOP (<http://wbiomed.curtin.edu.au/genepop/index.html>; Raymond and Rousset, 1995) was used to perform Fisher's exact tests for population pairwise  $F_{ST}$  and  $R_{ST}$  estimates with the null hypothesis being that the species/subspecies are not genetically differentiated. To examine isolation by distance we used Mantel tests within the sub-program Isolde (also implemented in GENEPOP).  $R_{IS}$  and  $R_{IT}$  were also calculated as indicators of occurrence of non-random mating processes.

#### *Fine scale genetic structure (Paper II)*

Pairwise relatedness estimates ( $r$ ) between males were calculated using the regression estimator of Lynch and Ritland (1999). Multi-dimensional scaling (MDS) was used to provide an unbiased representation of kin grouping on leks by transforming pairwise relatedness data to distance between points in two-dimensional space. Kin groupings produced by MDS were then compared with the actual court positions of males.

*Local genetic structure (Paper III)*

Population structure was analysed by running Bayesian analyses using the programs Structure (Pritchard et al., 2000) and Partition (Dawson and Belkhir, 2001). To calculate standard estimates of population divergence and inbreeding, we used Weir and Cockerham's (1984) formulation as implemented in Genetix 4.02 (Belkhir et al., 1996-2001). The program Parentage 1.0 (Wilson, 2000) was used to make inferences about family structure. To characterise the spatial genetic structure in the study area, we used the program AutocorG 1.2 Hardy and Vekemans, 2000). The parameters  $r$  (Ritland, 1996) and  $a_{ij}$  (Rousset, 2000) were calculated and plotted for different distance classes. F-statistics were also calculated using this program and produced estimates of inbreeding coefficients.

**Collection of behavioural and territorial data (Papers IV and V)**

During April-May 1998, March-May 1999 and February-April 2000 males on two leks were observed using hides. These were placed on opposite sides of each lek, about 30m from each other and about 5m from the outer court boundaries of the nearest male. Two observers made observations on male court ownership, male behaviour and mating success. In 1999 on two leks, detailed time budget recordings of display behaviours (fanning, snapping, grunt jumping, rolled snapping) and of aggression and chasing were made for each court-holding male using a hand-held PSION computer running The Observer (Noldus Information Technology, 1995). Observations of any court intrusions by other males or fights among males were noted. In 2000 on one lek only, detailed observations of male-male aggressive displays (Snow 1962) were made, with initiating and receiving males being identified. These were analysed with respect to groups of males showing low or high average pairwise relatedness values (Paper II). To assess if a male's court characteristics may have on mating success each was measured for size, distance from the lek

centre and number of saplings present. Also, any female visits to a males court were noted along with the time, whether the visits were made alone or in a group of females and whether the visits resulted in any matings.

## **RESULTS AND DISCUSSION**

### **Genetic divergence in the superspecies *Manacus* (Paper I)**

The term superspecies is used to describe a group of closely related species that appear similar but are distinct enough that differences are discernable (Mayr, 1963). Often, the classification of the various forms of a superspecies is in a state of confusion and authorities vary in their judgement of what should be named a species, a subspecies or when the observed variation should simply be ascribed to clinal variation. Classical studies on birds have, to a large extent, relied on plumage patterns in identifying populations within superspecies.

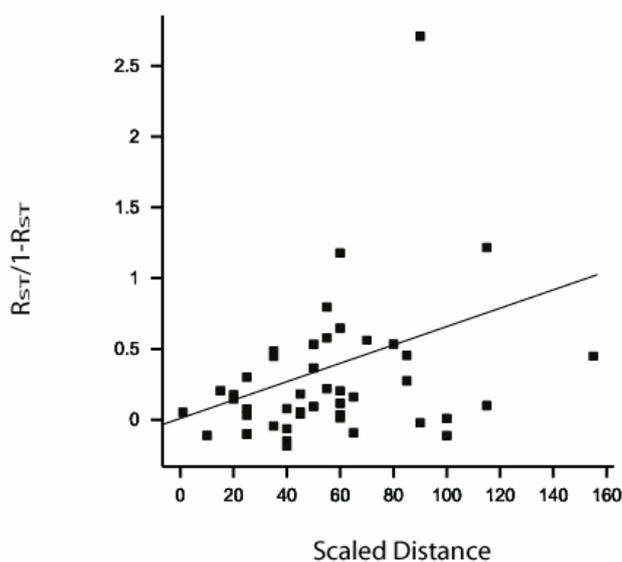
In this study we detected significant genetic differentiation among bearded manakin species/subspecies using the Fisher's exact tests implemented in GENEPOP ( $P$  for all loci combined for both genic and genotypic differentiation  $<0.001$ ) and could thus reject the null-hypothesis of no differentiation. All loci examined revealed significant genetic structure at  $\alpha < 0.001$ . The level of heterozygosity within the species/subspecies ( $R_{IS}$ ) was 0.05 ( $F_{IS} = 0.01$ ) and within all species/subspecies  $R_{IT}$  was 0.38 ( $F_{IT} = 0.06$ ) indicating non-random mating patterns.  $R_{ST}$  was 0.35 and population pair-wise  $R_{ST}$  and  $F_{ST}$  estimates (Table 1) indicated that there is significant genetic differentiation between any pair of species/subspecies in which we have reasonable sample sizes.

Analysis of isolation by distance did not detect a significant effect of geographic distance on genetic distance between species/subspecies (Mantel test,  $P=0.07$ ). However, the slope of geographic distance and  $R_{ST}/1-R_{ST}$  was positive (Figure 4). Hence, the possibility of a weak pattern of isolation by distance in bearded manakins should not be ruled out. Factors such as

geographic barriers may influence genetic structuring in bearded manakins. Accordingly, boundaries between species/subspecies often coincide with large rivers, mountains and sea (see Figure 1).

Table 1.  $R_{ST}$  and  $F_{ST}$  estimates for six pairs of bearded manakin species/subspecies and significance values calculated using Fisher's exact test.

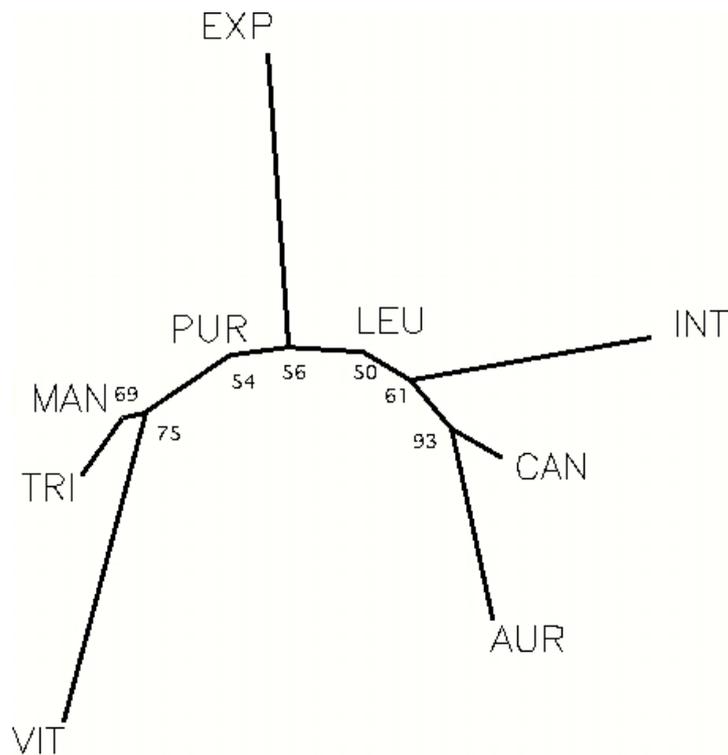
Pair	$R_{ST}$	$F_{ST}$	P
<i>candei-manacus</i>	0.22	0.09	<0.01
<i>candei-purus</i>	0.31	0.06	<0.01
<i>candei-trinitatis</i>	0.39	0.02	<0.01
<i>manacus-purus</i>	0.17	0.04	<0.01
<i>manacus-trinitatis</i>	0.07	0.03	<0.05
<i>purus-trinitatis</i>	0.33	0.03	<0.01



**Figure 4** The pairwise relationship between  $R_{ST}/1-R_{ST}$  and geographic distance among bearded manakin species/subspecies ( $R_{ST}/1-R_{ST} = 0.002 \times \text{distance}$ ).

The neighbour-joining phenogram suggests that species/subspecies from the Amazon basin/Ecuador form a central network (*purus*, *expectatus*, *leucochlamys* and *interior*) (Figure 5). A northeastern clade is formed by *manacus*, *trinitatis* and *vitellinus* and a northern clade by *candei* and *aurantiacus*.

Our findings of genetic divergence between bearded manakins suggest that some of the species/subspecies we have studied may render formal recognition as species. Indeed, *vitellinus*, *aurantiacus* and *candei* have been recognised as separate species from *manacus*. However, by giving some of the bearded manakins species status and others not, an artificial line of distinction is drawn between what seems to be a continuum of genetic divergence within the superspecies (Table 1).

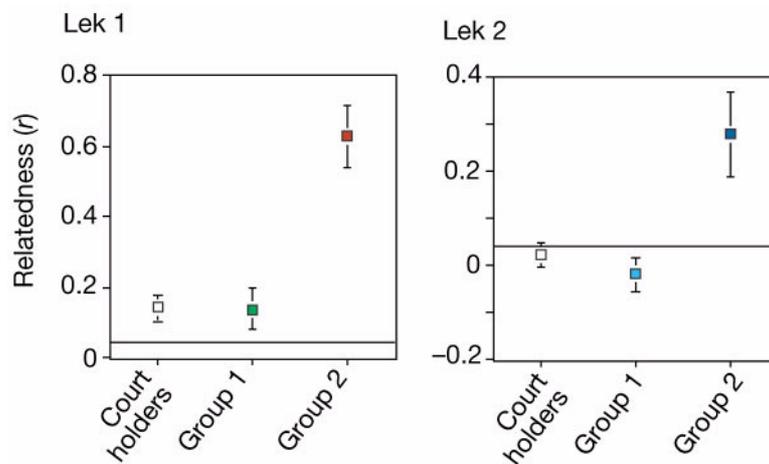


**Figure 5** Neighbour-joining phenogram depicting genetic distance relationships based on Nei's genetic distances ( $D_N$ ) among 9 bearded manakin species/subspecies. Values on nodes represent the percentage of bootstrap replicates over loci ( $n=1000$ ). Branch lengths are proportional to the genetic distance between species/subspecies. The distance between MAN and TRI corresponds to a  $D_N=0.12$ .

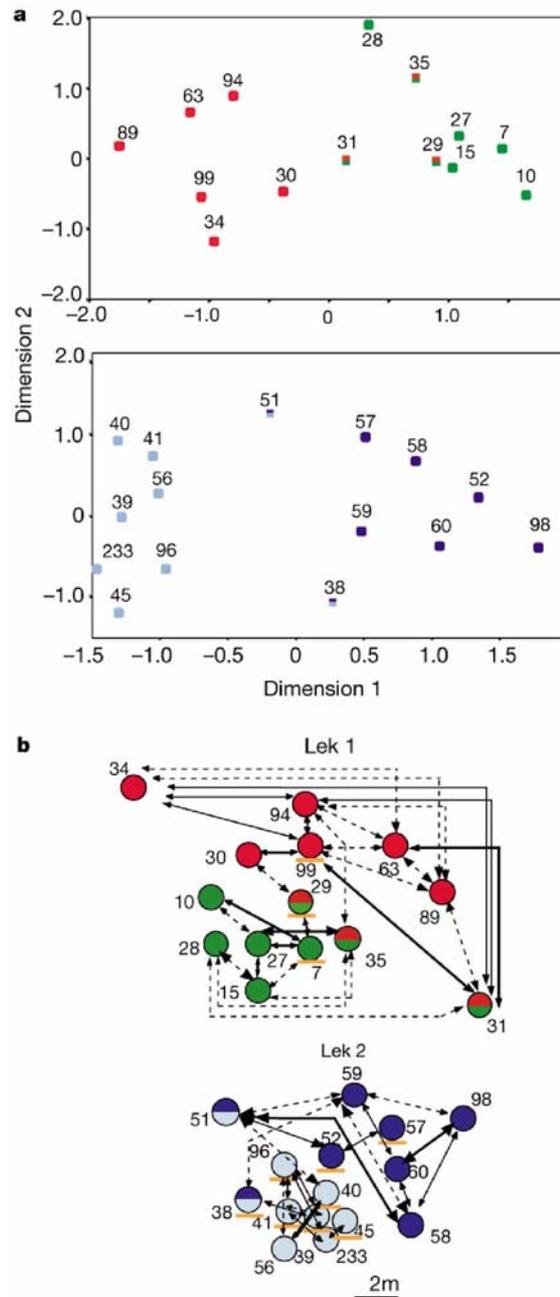
**Genetic structuring and the evolution of lekking behaviour in *Manacus manacus*:**

**Fine scale structuring (Paper II)**

Recent findings that in some bird species leks are kin structured (Höglund et al., 1999; Petrie et al., 1999; Shorey et al., 2000) have resulted in discussion of alternative hypotheses to the traditional views of lek formation. The results found in this study of white-bearded manakins show that leks are composed of clusters of related individuals. On each of two leks studied there was one group of closely related males and one group of less closely related males (Figures 6 and 7).



**Figure 6** Mean relatedness values of male groupings (bars indicate standard errors). The line in each graph indicates the mean relatedness of both leks. Legend: Green-group 1- Lek 1, Red- group 2- Lek 1, Light blue- group 1- Lek 2 and Dark blue-group 2- Lek 2. Statistics: ANOVA in all cases; Lek 1: Population vs. Court Holders,  $F_{1, 2158}=23.84$ ,  $P<0.0001$ ; Population vs. Group1,  $F_{1, 2082}=3.95$ ,  $P<0.047$ ; Population vs. Group2,  $F_{1, 2088}=153.3$ ,  $P<0.0001$ . Lek 2: Population vs. Court Holders,  $F_{1, 2172}=0.02$ , NS; Population vs. Group1,  $F_{1, 2094}=1.13$ , NS; Population vs. Group2,  $F_{1, 2088}=27.42$ ,  $P<0.0001$ .



**Figure 7** a) Multi-dimensional scaling of the  $r$ -values found on two *M. manacus* leks using a Euclidean distance model. b) Maps showing the positions of individual court holders on each lek. Arrows connect related males (bold arrows: significant at  $\alpha=0.05$ ; thin arrows:  $\alpha=0.25$ ; dashed arrows:  $r > 0.05$ , colour codes as in Fig. 6, males successful in obtaining copulations are underlined). We tested the spatial distribution of court holders by assigning them to one of either group found at each lek. Disregarding males spanning two groups, the observed spatial distribution of males was highly non-random (Fisher's exact test: Lek1,  $P=0.002$ ; Lek2,  $P=0.00058$ ). Males with two colours were related to both groups.

We suggest that such aggregation of relatives will allow inclusive fitness benefits mediated through kin selection to operate (Hamilton, 1964). That is, by aggregating in this way an individual could enhance his own inclusive fitness by joining a lek where a relative is dominant and increasing this individual's reproductive success. Relatives may be more likely to gather around a top male and be accepted if they help in the initial attraction of females to the lek. By clustering near a top male, a family member may also improve his chances of acquiring a central court in the case of death or injury of his successful relative.

By forming related groups within leks, it seems that establishment on *M. manacus* leks cannot simply be attributed to limited male natal dispersal where males join the lek closest to their place of birth. Once on the lek, active choice among residential and newly arrived birds must take place (Sherman, 1999) since we observed clusters of relatives within leks. As suggested by our data, there may be more than one such family group on a single lek.

It is unlikely that individuals learn the characteristics of their relatives in the nest since clutch size is only one or two eggs in *M. manacus* and nest predation is high (Snow, 1962). Thus any male surviving to become an adult is unlikely to have shared the nest with any other bird in the population. The most plausible mechanism is that both prospecting floaters and established court-holders use some kind of phenotype matching (Sherman et al., 1997) such as self-referent phenotype matching (Hauber and Sherman, 2001) when juveniles float around the leks in the local population before settling on a lek.

This study adds support to the proposed hypothesis of kin-selection being involved in lek evolution and highlights a paradigm-shift away from the view that leks are primarily arenas for intra-sexual competition. Moreover, our data suggests that wild populations that have previously been thought of as being composed of unrelated individuals can be kin-structured at a very fine level, and this structure can have profound effects on reproductive success.

### **Local genetic structuring (Paper III)**

In understanding the evolutionary causes of social behaviour as well as its effects on population genetic structure it is important to identify the proper level of population structure (Ross, 2001). When linking properties of the breeding group structure to group composition and genetic structure, larger scale population genetic properties (such as metapopulation diversity and structure) have been emphasised (Sugg et al., 1996). On a more local scale, further hierarchical levels than subpopulations may be present if social structures are present (Piertney et al., 1998; Piertney et al., 1999; MacColl et al., 2000). Examples of such social structures may be social insect colonies (e.g. Ross, 1993; Sundström, 1993; Seppä, 1994) and local breeding groups in some rodents (Hoogland, 1992). Here we looked at kin structure and inbreeding coefficients in a free ranging population of white-bearded manakins.

#### *Number of populations*

Assuming that leks correspond to spatial subpopulations we could not detect any significant divergence between them ( $F_{ST}=0.001$ , NS). Using Structure we found that the posterior probability for  $K=1$  (one genetic population, i.e. no departure from Hardy Weinberg) was very close to one and hence the posterior probabilities for the alternatives considered ( $K$  being 2, 3, 4, 5, 6 and 9 respectively) were almost 0. Using Partition we found that the posterior probability of  $K=1$  was 0.96 and that the alternatives hence had low probabilities ( $K=2$ ,  $P=0.02$ ;  $K=3$ ,  $P=0.01$  and  $K=4$ ,  $P=0.01$ ). The Bayes factor was 69.98. If the Bayes factor is greater than 1, this means that the evidence favours the hypothesis that  $K=1$ .

#### *Lek structure*

The average number of birds caught on each lek was 26.4. Of these, 20.3 were male birds in nuptial plumage, 3.4 were females and 2.6 were males in juvenile/female-like plumage. Using Parentage we found on average 14.9 half-

sib and 2 full-sib relationships per lek. On the two leks with behavioural data we found that 14 (of a possible 40 males) and 15 (of a possible 26 males) were defending permanent territories (these numbers are for 1998 only).

*Spatial autocorrelations within the population*

The inbreeding coefficient indicating non-random mating in the total population ( $F_{IT}$ ) was 0.02 ( $P=0.0015$ ) and in relation to subpopulations ( $F_{IS}$ - where S is leks) was 0.02 ( $P=0.002$ ) (see also Figure 8a). We could not detect any significant population sub-division ( $F_{ST}$ ). Comparing individuals within leks revealed an average kinship coefficient significantly greater than zero, which decreased with the distance at which individual relationships were compared (Figure 8a). When we applied a similar analysis to the parameter  $a_{ij}$ , we observed a high pair-wise divergence between individuals within leks, which dropped at a distance of 1 km and then increased with increasing distance to finally level off (Figure 8b).

That kinship coefficients decreased with increasing geographic distance indicated that related birds displayed at the same lek. However, leks do not consist of only one kin group since the average genetic distance ( $a_r$ ) between males among leks was higher than when comparing males on leks within close proximity. As with kinship coefficients, we found that the genetic similarity decreased with genetic distance. We interpret these patterns as an effect of kin recognition and that males on leks are more likely to establish themselves as territorial birds if they have a relative already present.

Fig.8a

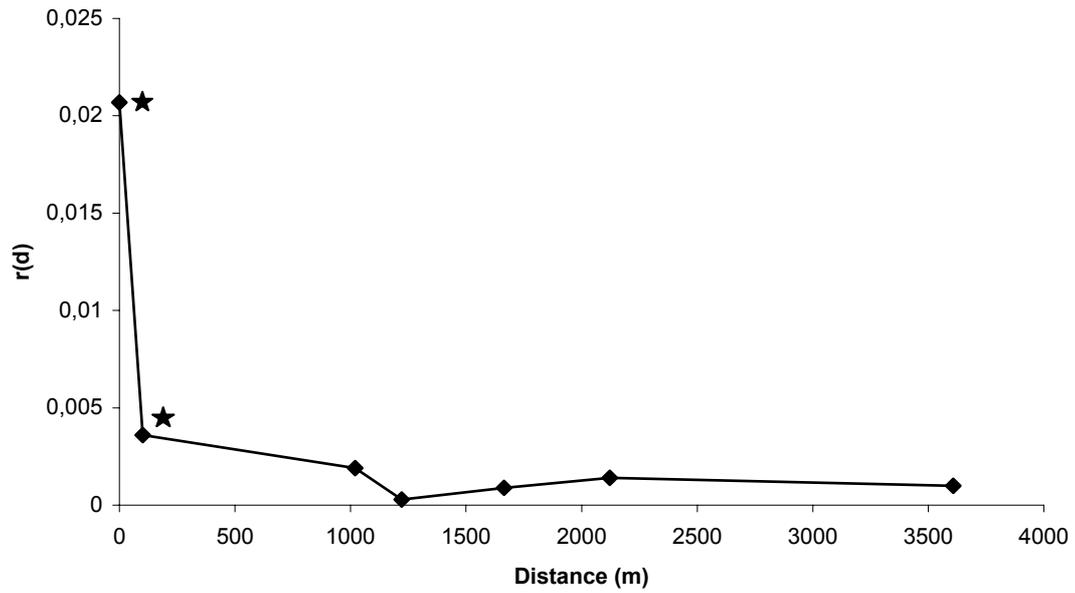
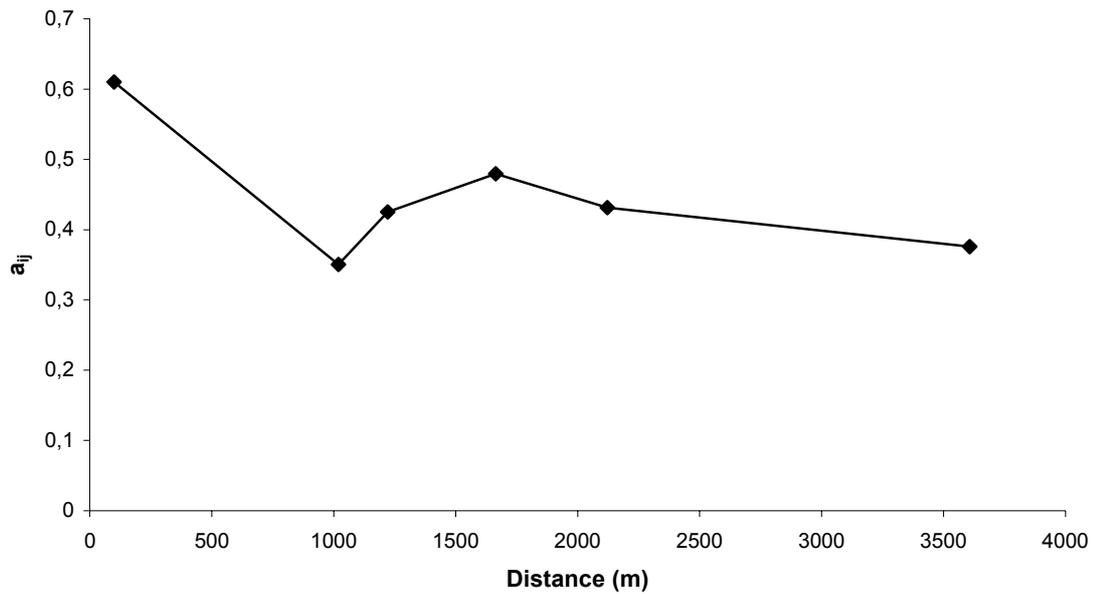


Fig.8b



**Figure 8** a). Kinship coefficients as a function of distance between individuals. The point at distance  $x=0$  corresponds to  $F_{IS}$ . Stars indicate that estimates are different from 0. b) Genetic distance between individuals ( $a_{ij}$ ) as a function of geographic distance between individuals. All estimates are significant.

**Mating success on white-bearded manakin (*Manacus manacus*) leks: male characteristics and relatedness (Paper IV)**

High variance in male mating success is a typical feature of lekking systems and has been observed in many species (for reviews, see Bradbury et al., 1985; Wiley, 1991; Höglund and Alatalo, 1995) including the white bearded manakin (Lill, 1974). Much work has been done on other lekking birds to assess which factors may be important in determining male mating success. Those include morphological, behavioural and territorial characteristics (e.g. Fiske et al., 1994; Hill, 1991; Apollonio et al., 1989). The combined effect of several factors may play an important role in influencing individual mating success (Höglund and Alatalo, 1995) and factors may be mediated by both male-male competition and/or female preferences (Gibson and Bradbury, 1986; Höglund et al., 1997).

The genetic structuring seen on white-bearded manakin leks may affect how matings are distributed among males. Factors such as kinship and male-male interactions may influence patterns of mating distribution. Indeed, the importance of male social dominance in the development of lek mating systems and female mate choice has previously been suggested (Gibson and Bradbury, 1986; Beehler and Foster, 1988). In Paper IV I tested whether morphological, behavioural (display) or territorial characteristics are correlated with mating success on two white-bearded manakin leks and investigated whether patterns of aggression between males vary with pairwise relatedness levels.

*Morphological data*

When combining morphological data obtained from males on Leks 1 and 2 (1999) in a principal components analysis, tarsus had the highest loadings in the first principal component (PC1) of morphologies. Bill length had the highest loading in the second principal component (PC2) (data not shown).

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## *Genetic Structuring and the Evolution of Lekking Behaviour*

PC1 significantly correlated with mating success in the combined data from Leks 1 and 2 in 1999 (Table 2). There was no significant correlation between PC2 and mating success ( $r=0.08$ ,  $n=26$ ,  $p=0.73$ ,  $\beta=0.1$ ). Condition was significantly correlated with mating success in 1999 (Table 2).

### *Territorial data*

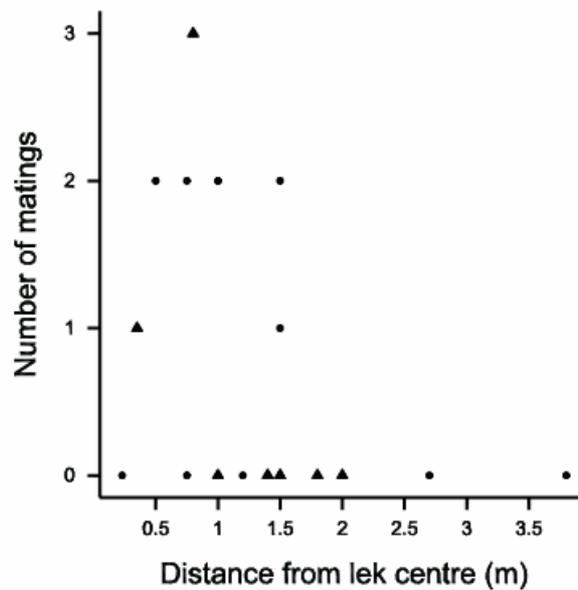
In a multiple regression of territorial factors, distance to the lek centre is seen to correlate with mating success (Table 3, Figure 9).

Table 2. Results of correlation analyses: morphological variables and mating success. Size and condition were significantly correlated with mating success in 1999.

Variables	r	n	p	$\beta$
PC1 “size” Leks 1&2 1999	0.47	26	0.01	0.84
PC1 “size” Lek 2 1999	0.38	16	0.09	0.47
PC1 “size” Lek 2 2000	-0.06	14	0.85	0.08
Condition 1999	0.57	19	0.01	0.89
Condition 2000	0.34	14	0.24	0.36

Table 3. Results of a multiple regression of territorial factors with mating success. Distance to the lek centre is correlated with mating success.

Variables	t	n	p
<b>Lek 2 2000</b>			
Distance to lek centre	-2.24	15	0.038
Court area	1.12	15	0.426
No. of saplings on court	-1.32	15	0.964



**Figure 9** Actual number of matings gained per male and distance of each respective male court from the lek centre (Log transformed values were used in analysis). Triangles=Lek 1, Circles=Lek 2.

*Behavioural data*

When combining behavioural time budget data obtained from all court holding males on Leks 1 and 2 (1999) in a principal components analysis, grunting and snapping had the highest loadings in the first principal component (PC1) of male “behaviour”. Aggressive display and chasing had the highest loading in the second principal component (PC2) (Table 4). PC1 showed no significant correlation with mating success whereas PC2 showed a significant correlation (Table 5). There was no significant effect of total duration of activity of a bird or in the total time a male spent in display behaviour on mating success (Table 5).

Table 4. Component loadings of behavioural variables (duration) as quantified by principal components analysis (n=26).

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Trait	PC1	PC2
Aggressive display	-0.14	0.71
Chasing	0.13	0.69
Fanning	0.42	0.12
Grunting	0.59	-0.05
Rolled snapping	0.35	-0.001
Snapping	0.56	-0.03
Eigenvalues	2.495	1.493
% of variance explained	41.58	24.88

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Table 5. Results of correlation analyses: behavioural variables (duration) with mating success.

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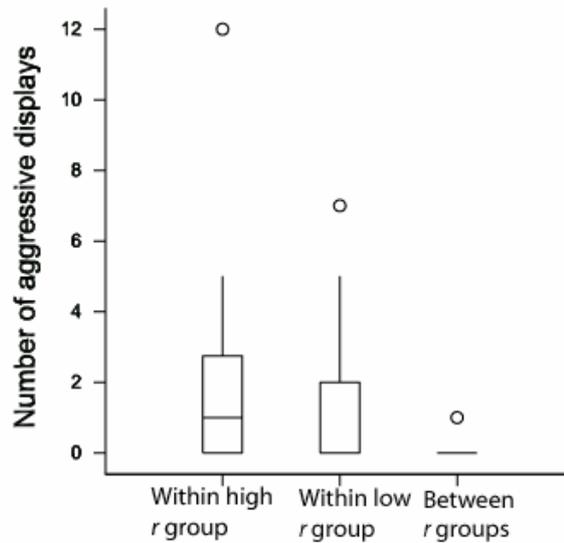
Variables	r	n	p	$\beta$
<b>Leks 1 &amp; 2 1999</b>				
PC1 “display”	0.32	26	0.118	0.51
PC2 “aggression”	0.49	26	0.011	0.87
Aggression	0.47	26	0.015	0.84
Total time in activity	0.09	26	0.655	0.12
Total time displaying	0.25	26	0.205	0.36
<b>Lek 2 1999</b>				
Aggression: (Low <i>r</i> )	0.18	7	0.699	0.11
(High <i>r</i> )	0.22	6	0.922	0.12

---

Aggressive displays between males were few but correlated with decreasing distance between male courts ( $r = -0.25$ ,  $n = 15$ ,  $p = 0.006$ , Figure 10). When behavioural data were analysed in groups of low  $r$  and high  $r$  males, the total duration a male spent in aggressive behaviour was not correlated in either group (Table 5). More aggressive displays were made between males within the high  $r$  group than between males in the low  $r$  group ( $\chi^2 = 5.80$ ,  $df = 1$ ,  $p = 0.016$ ). More displays were made within the groups than between groups ( $\chi^2 = 25.82$ ,  $df = 2$ ,  $p < 0.001$ , Figure 11). In a partial mantel test there was no significant relationship between number of aggressive displays and pairwise  $r$  values ( $r = 0.12$ ,  $p = 0.38$ ).



**Figure 10** The relationship between the number of pairwise aggressive displays  $n = 105$  (corrected for observational time) and the distance between their respective courts. Number of aggressions increased as distance between courts decreased.



**Figure 11** Number of aggressive displays between males within the high and low *r* groups (see text) and between the two fore-mentioned groups (corrected for observational time). The boxes contain values falling between the 25<sup>th</sup> and 75<sup>th</sup> percentiles. The line across the box indicates the median. Lines extending above the box show 90<sup>th</sup> percentiles. Circles show outliers above and below the 90<sup>th</sup> and 10<sup>th</sup> percentiles. These results remained significant even when the outlier in the high *r* group was removed.

It appears that mating success in the white-bearded manakin is most likely mediated by a combination of morphological and behavioural characteristics, influencing both male-male competition and female choice and changing over seasonal time. Dominance factors may play an important role in influencing mate selection. These traits must be manifested through behavioural differences in order to be selected, either through male-male competition or female preference (Höglund et al., 1997). Centrality on the lek may be an important indicator of such dominance. Pairwise relatedness may influence spatial arrangement of males on a lek thereby affecting male-male displays and ultimately influencing patterns of mating success.

**Female visiting patterns in the white-bearded manakin *Manacus manacus*: potential for mate-choice copying (Paper V)**

The extreme biases in the distribution of male matings on leks have largely been interpreted as evidence of sexual selection through female choice. Distributions of matings do not however address which mechanisms (e.g. female choice, male-male competition, copying etc.) generate the observed mating pattern. Mate-choice copying may potentially be important in helping to explain why in leks, females show an extreme bias towards only a few of the available mates (van Rhijn, 1973; Wiley, 1973; Lill, 1974). Indeed, experimental evidence of female copying has been found in some lekking species (Gibson et al., 1991; Höglund et al., 1995).

Recently, Sirot (2001) presented a simple genetic and behavioural model suggesting that mate-copying behaviour could have been selected for because it reduces the genetic risk for breeding females by preventing any particular female from being the only one in the population that has chosen the ‘wrong’ father for her offspring. Also, as reproductive success is relative in terms of other females, it is important to consider that the descendants of a particular female will have to compete with those of other females, and this may influence female choice. Furthermore, the offspring of females that reproduce synchronously and in the same place will more often compete with each other. Therefore, mate-choice copying may be a ‘prudent’ strategy. White-bearded manakin females have a localised synchrony in breeding, with nests near any one particular display ground tending to be better synchronized with each other than with those at other display grounds (Snow, 1962). Furthermore, females encountering males of apparent similar phenotype may have difficulty in assessing real quality between individuals. In this case, females may choose to mate with males they have observed mating, or that they have observed other females associating with (Sirot, 2001; White and Galef, 2000). This may be of relevance in white-bearded manakins where leks have been shown to consist of groups of closely related males (Shorey et al., 2000).

In Paper V I looked at the distribution of female visits and mate choice among court holding males on a white-bearded manakin lek. I considered the temporal and diurnal distribution of visits to the lek by females and matings observed. I also tested if those males receiving more group visits from females gain more matings, which would infer the potential for female copying of mate choice.

*Distribution of female visits*

The distribution of female visits was more skewed towards a few males than expected from a random Poisson distribution. Under a Poisson assumption each female visits a male at random. This null model can be rejected (Kolmogorov Smirnov test;  $d=0.37$ ,  $n=15$ ,  $p<0.01$ ). There was a peak of female visits to the lek early in the season (Figure 12a). The majority of female visits were made to the lek between 06.30 and 07.30 (Figure 13). There was no significant effect of centrality on the number of group or single visits, although there was a trend for females to make more group visits to central territories (number of group female visits/distance of court from lek centre:  $t=-1.44$ ,  $n=15$ ,  $p=0.15$ ,  $\beta=0.61$ , number of single female visits/distance of court from lek centre:  $t=0.43$ ,  $n=15$ ,  $p=0.67$ ,  $\beta=0.59$ ).

*Distribution of matings*

The distribution of matings was more skewed towards a few males than expected from a random Poisson distribution (Kolmogorov Smirnov test;  $d=0.31$ ,  $n=15$ ,  $p<0.01$ ). There was a peak of matings early in the season (Figure 12b). The majority of matings took place between 06.30 and 07.30 (Figure 13).

Fig. 12a

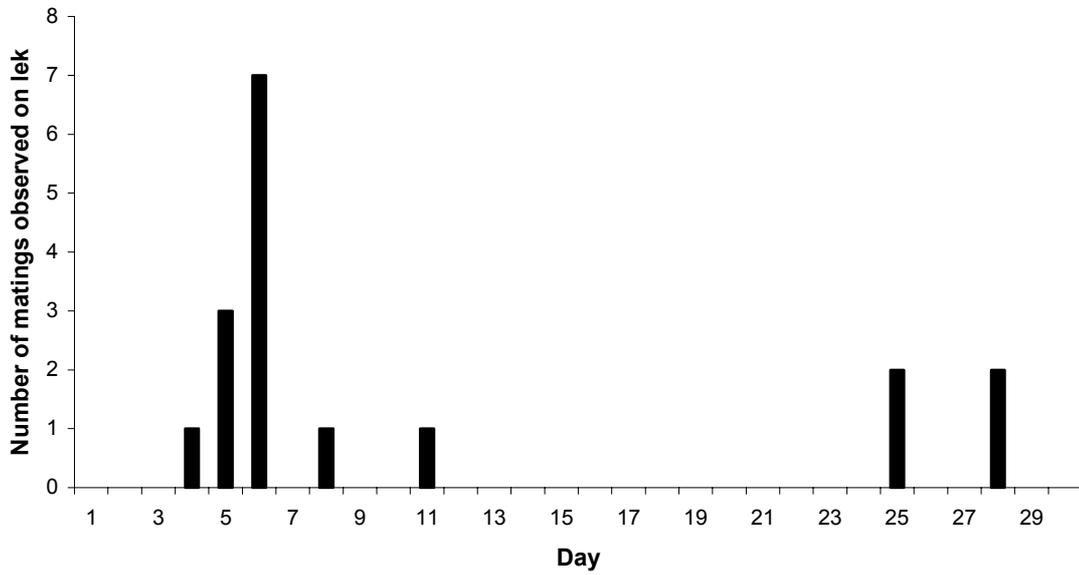
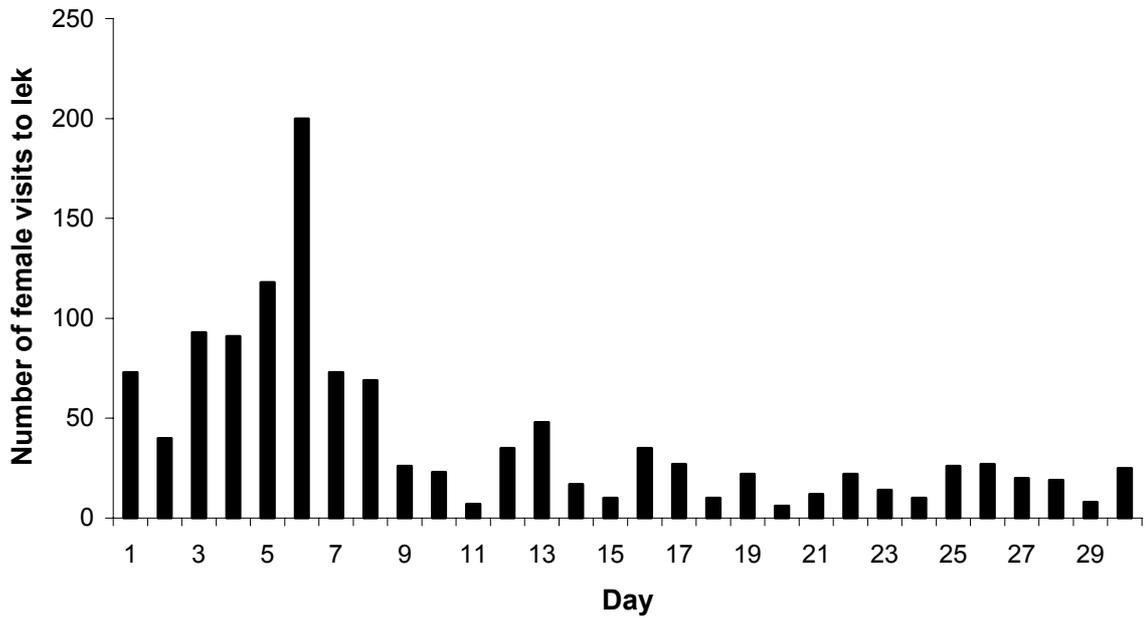
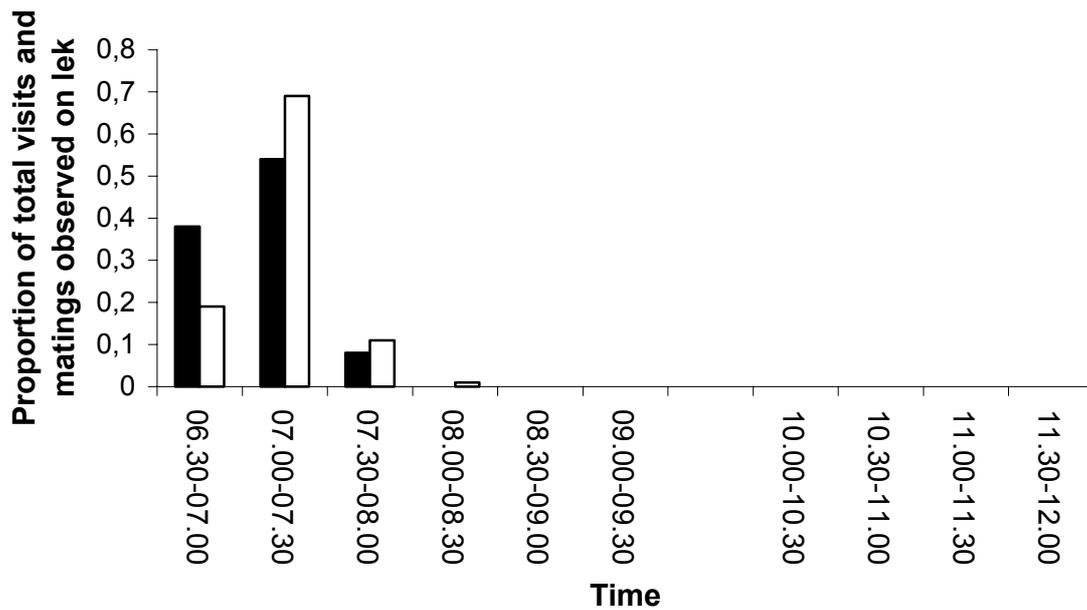


Fig. 12b



**Figure 12** a) The distribution of female visits to the lek over the observation period.  
b) The number of matings observed on the lek over the observation period



**Figure 13** The distribution of matings (shaded) and female visits (unshaded) within the daily observation times. Data corrected for observation time.

The number of single and group female visits to the lek per day correlated with the number of matings per day (cops/single visits/day:  $t=3.06$ ,  $n=30$ ,  $p<0.01$ ; cops/group visits/day:  $t=2.32$ ,  $n=30$ ,  $p<0.05$ ). When considering individual male mating success there was no apparent relationship of single visits with mating success ( $t=0.23$ ,  $n=15$ ,  $p=0.82$ , power of analyses ( $\beta$ ) = 0.24). However, there was a significant relationship between group visits and mating success ( $t=2.2$ ,  $n=15$ ,  $p<0.05$ ).

Female visiting patterns and mating distributions among court holding males were non-random. Such a skew is common in lekking species (Höglund and Alatalo, 1995). That a peak of visits and matings was seen towards the beginning of the observation period may indicate that females are under some time-constraint in way of food abundance for chicks. In relation to food supply, the breeding season starts at some time in the period when fruit and insects are most abundant (Snow, 1962). There is, however, no regularly recurring period

of food shortage like that which plays such an important part in the ecology of northern birds (Snow, 1962).

That the number of group visits but not single visits by females to a male correlated with his mating success suggests that female mate-choice copying could possibly occur in this species. However, the low power of the relationship between single visits and matings makes the interpretation of this result ambiguous. It is thus difficult to show that copying exists by purely observational data. Additionally, one cannot exclude other possibilities, such as males increasing display rate in the presence of females or after mating (Lill, 1974; Pruett-Jones, 1992), male-male competition (Foster, 1977; 1981; Beehler and Foster, 1988; Trail, 1990; McDonald, 1989; 1990) or female choice (Parker, 1983; Partridge and Halliday, 1984; Gibson and Bradbury, 1986). However, the patterns seen in this study support the possibility of mate-choice copying in this lekking species.

## **CONCLUSIONS**

Leks have traditionally been considered as arenas for intrasexual competition that have evolved primarily through direct fitness benefits to each individual male. However, the recent discovery that leks of some bird species consist of related individuals has brought about an alternative view to the mechanisms traditionally thought to drive lek evolution.

This study has made use of molecular and behavioural data to identify factors driving or influencing lek evolution in the white-bearded manakin. The results show that within leks, white-bearded manakin males cluster in groups of related individuals. There may be more than one group of related individuals on each lek. This indicates that dispersal must be limited so that relatives do meet but that additionally there is likely to be some form of kin recognition. Within leks, the spatial arrangement of kin and non-kin and the behavioural interactions that take place between and among them may influence the evolution of the lek and affect the distribution of male mating success. However, the formation and functioning of the lek can be influenced by a complex interaction between a number of variables.

The presence of social structuring has previously been realised as important in the study of evolutionary processes and has recently been studied in some organisms such as social insects and rodents. However, if structuring is overlooked our understanding of these processes could be distorted. Indeed, if molecular or behavioural data are looked at in isolation important patterns may be missed.

It may be that kin structuring is not found in all lekking species. Although many species form leks, the underlying processes in the formation of these aggregations are not known and may vary widely between species. Given the profound differences among many of the lekking species it is probably not possible to find a single explanation for the evolution of lekking behaviour that is applicable across all species.

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## REFERENCES

- American Ornithologists Union. 1983. Checklist of North American Birds, 6<sup>th</sup> ed.
- Apollonio M, Festa-Bianchet M, Mari F. 1989. Correlates of copulatory success in a fallow deer lek. *Behav Ecol Sociobiol* 25: 89-97
- Balloux F, Lugon-Moulin N. 2002. The estimation of population differentiation with microsatellite markers. *Mol Ecol* 11: 155-165
- Beehler BM, Foster MS. 1988. Hotshots, hotspots, and female preference in the organization of lek mating systems. *Am Nat* 131: 203-219
- Belkhir, K Borsa P, Chikhi L, Raufaste N, Bonhomme F. 1996-2001. GENETIX 4.02, logiciel sous Windows TM pour la génétique des populations. Laboratoire Génome, Populations, Interactions, CNRS UMR 5000, Université de Montpellier II, Montpellier, France
- Bradbury JW, Vehrencamp SL, Gibson R. 1985. Leks and the unanimity of female choice. In: Greenwood PJ, Harvey PH, Slatkin M (eds) *Evolution: Essays in Honour of John Maynard Smith*. Cambridge University Press, Cambridge UK. pp 301-314
- Cornuet JM, Luikart G. 1996. Description and power analysis of two tests for detecting recent population bottlenecks from allele frequency data. *Genetics* 144: 2001-2014
- Dawson KJ, Belkhir K. 2001. A Bayesian approach to the identification of panmictic populations and the assignment of individuals. *Genet Res Camb* 78: 59-77
- Dobson FS. 1982. Competition for mates and predominant juvenile dispersal in mammals. *Anim Behav* 30: 1183-1192
- Emlen ST, Oring LW. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197: 215-223
- Felsenstein J. 1993. PHYLIP (Phylogeny Inference Package) manual, version 3.5c. University of Washington Press, Seattle
- Fiske P, Kålås, JA, Saether SA. 1994. Correlates of male mating success in the lekking great snipe (*Gallinago media*): results from a four year study. *Behav Ecol* 5 (2): 210-218

- Foster MS. 1977. Odd couples in manakins: a study of social organization and cooperative breeding in *Chiroxiphia linearis*. *Am Nat* 111: 845-853
- Foster MS. 1981. Cooperative behaviour and social organization of the swallow-tailed manakin (*Chiroxiphia caudata*). *Behav Ecol Sociobiol* 9: 167-177
- Gibson RM, Bradbury JW. 1986. Male and Female Mating Strategies on Sage Grouse Leks. In: Rubenstein DI, Wrangham RW (eds) *Ecological Aspects of Social Evolution*. Princeton University Press, New Jersey, pp 379-398
- Gibson R, Bradbury J, Vehrencamp S. 1991. Mate choice cues in sage grouse revisited: the role of male display and territory location. *Behav Ecol* 2: 165-180
- Greenwood PJ. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Anim Behav* 28: 1140-1162
- Griffiths R, Double MC, Orr K, Dawson RJG. 1998. A DNA test to sex most birds. *Mol Ecol* 7: 1071-1075
- Griffiths R, Orr K. 1999. The use of amplified fragment length polymorphism (AFLP) in the isolation of sex-specific markers. *Mol Ecol* 8: 671-674
- Hamilton WD. 1964. The genetical evolution of social behaviour I. *J Theor Biol* 7: 1-16
- Hardy OJ. & Vekemans X. 2002. SPAGeDi 0.0 a program for spatial pattern analysis of genetic diversity. [ohardy@ulb.ac.be](mailto:ohardy@ulb.ac.be)
- Hauber ME, Sherman PW. 2001. Self-referent phenotype matching: theoretical considerations and empirical evidence. *Trends in Neurosciences* 24: 609-616
- Hedrick PW. 1999. Perspective: Highly variable loci and their interpretation in evolution and conservation. *Evolution* 53: 313-318
- Hill WL. 1991. Correlates of male mating success in the ruff *Philomachus pugnax*, a lekking shorebird. *Behav Ecol Sociobiol* 29: 367-372
- Hoogland JL. 1992. Levels of inbreeding among prairie dogs. *Am Nat* 139: 591-602
- Höglund J, Alatalo RV. 1995. *Leks*. Princeton University Press, Princeton, New Jersey

- Höglund J, Alatalo RV, Gibson RM, Lundberg A. 1995. Mate choice copying in black grouse. *Anim Behav* 49: 1627-1633
- Höglund J, Johansson T, Pelabon C. 1997. Behaviourally mediated sexual selection: characteristics of successful male black grouse. *Anim Behav* 54: 255-264
- Höglund J, Alatalo RV, Lundberg A, Rintamäki PT, Lindell J. 1999. Microsatellite markers reveal the potential for kin selection on black grouse leks. *Proc Roy Soc Lond B* 266: 813-816
- Kokko H, Lindström J. 1996. Kin selection and the evolution of leks: whose success do young males maximise? *Proc Roy Soc Lond B* 263: 919-923
- Kricher J. 1997. *A Neotropical Companion: an introduction to the animals, plants, and ecosystems of the New World tropics*. 2<sup>nd</sup> ed. Princeton University press, Princeton, New Jersey
- Lill A. 1974. Sexual behaviour of the lek forming white-bearded manakin, *M. manacus trinitatis*. *Z Tierpsychol* 36:1-36
- Lowe PR. 1942. The anatomy of Gould's manakin (*Manacus vitellinus*) in relation to its display. *Ibis* 14 (6): 50-83
- Lynch M, Ritland K. 1999. Estimation of pairwise relatedness with molecular markers. *Genetics* 152: 1753-1766
- MacColl CA, Alonso, JC, Alonso, J, Pitra C, Lieckfeldt D. 2000. Spatial arrangement of kin affects recruitment success in young male red grouse. *Oikos* 90: 261-271
- Maniatis T, Fritsch EF, Sambrook J. 1982. *Molecular cloning. A Laboratory Manual*. Cold Spring Harbor Press, New York
- Mayr E. 1963. *Animal species and evolution*. Belknap Press, Cambridge MA
- McDonald DB. 1989. Cooperation under sexual selection: Age-graded changes in a lekking bird. *Am Nat* 134: 709-730
- McDonald DB. 1990. Correlates of male mating success in a lekking bird with male-male cooperation. *Anim Behav* 37: 1007-1022
- Noldus Information Technology. 1995. *The Observer, Base Package for the Macintosh. Reference Manual, version 3.0 Edition*. Wageningen, The Netherlands

Parker GA. 1983. Mate quality and mating decisions. In: Bateson P (ed). *Mate Choice*. Cambridge University Press, UK. pp 141-166

Partridge L, Halliday T. 1984. Mating patterns and mate choice. In: Krebs JR, Davies NB (eds). *Behavioural Ecology: An Evolutionary Approach*. Blackwell Press, Oxford, UK. pp 222-250

Peters JL. 1951-1970. *Checklist of the Birds of the World*, vols.7-15. Cambridge, Mass.: Museum of Comparative Zoology

Petrie M, Krupa A, Burke T. 1999. Peacocks lek with relatives even in the absence of social and environmental cues. *Nature* 401: 155-157

Piertney SB, MacColl ADC, Bacon PJ, Dallas JF. 1998. Local genetic structure in red grouse (*Lagopus lagopus scoticus*): evidence from microsatellite data. *Mol Ecol* 7: 1645-1654

Piertney SB, MacColl ADC, Lambin X, Moss R, Dallas JF. 1999. Spatial distribution of genetic relatedness in a morrland population of red grouse (*Lagopus lagopus scoticus*). *Biol J Linn Soc* 68: 317-331

Pruett-Jones S. 1992. Independent versus nonindependent mate choice: Do females copy each other? *Am Nat* 140 (6): 1000-1009

Prum RO. 1994. Phylogenetic analysis of the evolution of alternative social behavior in the manakins (Aves:Pipridae). *Evolution* 48: 1657-1653

Pritchard JK, Stephens M, Donnelly P. 2000. Inference of population structure using multilocus genotype data. *Genetics* 155: 945-959

Raymond M, Rousset F. 1995. Genepop (Version 3.1d): population genetics software for exact tests and ecumenism. *Journal of Heredity* 86: 248-249

Ridgely RS, Tudor G. 1994. *The birds of South America*. Oxford University Press, Oxford

Ritland K. 1996. A marker based method for inferences about quantitative inheritance in natural populations. *Evolution* 50: 1062-1073

Ross KG. 1993. The breeding system of fire ant *Solenopsis invicta*: effects of colony genetic structure. *Am Nat* 141: 554-576

Ross KG. 2001. Molecular ecology of social behaviour: analyses of breeding systems and genetic structure. *Mol Ecol* 10: 265-284

Rousset F. 2000. Genetic differentiation between individuals. *J Evol Biol* 13: 58-62

Saiki RK, Scharf S, Faloona F et al. 1985. Enzymatic amplification of beta-globin genomic sequences and restriction site analysis for diagnosis of sickle cell anaemia. *Science* 230: 1350-1354

Seppä P. 1994. Sociogenetic organization of the ants *Myrmica ruginodis* and *Myrmica lobicornis*: number, relatedness and longevity of reproducing individuals. *J Evol Biol* 7: 71-95

Sherman PW, Reeve HK, Pfennig DW. 1997. In: *Behavioural Ecology An Evolutionary Approach* 4<sup>th</sup> edn (Krebs JR, Davies NB eds) Blackwell, Oxford pp 69-96

Sherman PW. 1999. Birds of a feather lek together. *Nature* 401: 119-120

Shorey L, Piertney S, Stone J, Höglund J. 2000. Fine-scale genetic structuring on *Manacus manacus* leks. *Nature* 408: 352-353

Sick H. 1967. Courtship behavior in manakins (Pipridae): A review. *Living Bird* 6: 5-22

Sirot E. 2001. Mate-choice copying by females: the advantages of a prudent strategy. *J Evol Biol* 14: 418-423

Snow DW. 1962. A field study of the black and white manakin, *Manacus manacus*, in Trinidad. *Zoologica* 47: 65-104

Sugg DW, Chesser RK, Dobson FS, Hoogland JL. 1996. Population genetics meets behavioural ecology. *TREE* 11(8): 338-342

Sundström L (1993) Genetic population structure and sociogenetic organisation in *Formica truncorum* (Hymenoptera; Formicidae). *Behavioral Ecology and Sociobiology* 33: 345-354

Thornhill R, Alcock J. 1983. *The Evolution of Insect Mating Systems*. Harvard University Press

Thornhill NW (ed).1993. *The Natural History of Inbreeding and Outbreeding: Theoretical and Empirical perspectives*. University of Chicago Press

Trail PW. 1990. Why should lek-breeders be monomorphic? *Evolution* 44: 1837-1852

Van Rhijn JG. 1973. Behavioural dimorphism in the ruff *Philomachus pugnax*. *Ibis* 125: 482-498

Weir BS, Cockerham CC. 1984. Estimating F-statistics for the analysis of population structure. *Evolution* 38: 1358-1370

White DL, Galef BG. 2000. 'Culture' in quail: social influences on mate choices of female *Coturnix japonica*. *Anim Behav* 59: 975-979

Wiley RH. 1973. Territoriality and non-random mating in sage grouse, *Centrocercus urophasianus*, *Anim Behav Monogr* 6: 87-169

Wiley RH. 1991. Lekking in birds and mammals: Behavioural and evolutionary issues. *Adv Study Behav* 20: 201-291

Wilson I. 2000. Parentage vers. 1.0 Users guide.  
<http://www.maths.abdn.ac.uk/~ijw>