



ARTICLES

Social organization and variation in cooperative alliances among male lance-tailed manakins

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In species where males form cooperative alliances for the purposes of reproduction, there may be considerable variation in the strength and size of alliances observed within one population. Male lance-tailed manakins, *Chiroxiphia lanceolata*, form long-term cooperative alliances to court females on group-occupied display areas. I investigated male status and alliance structure in a colour-banded population. Each display area was a group territory attended by multiple adult and subadult males. Alpha males were present at display areas more often than other males, performed solo courtship displays for females, and vocalized distinctively in paired displays. Alpha–beta pairs had high duetting association index values and performed two types of paired courtship displays for females. I combined these characteristics in a predictive logistic regression model to assess male status probabilistically when not all key behaviours were observed. Typically, one alpha and one beta male occupied each display area, but males also formed multiple alliances (one alpha paired with multiple high-ranking subordinates) or were solitary, with no distinct alliances. Both alliances and solitary alphas attracted females for courtship displays. Alphas were generally older than their beta partners, but age did not absolutely predict status. Individual alpha males were involved in different alliance types in different years, showing that alliance variation is not the result of fixed differences in individual strategies. Instead, variation apparently results from changing opportunities for partnership formation and territory acquisition.

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Alliances are a form of cooperation in which individuals work together to compete with conspecifics for resources. Males of a variety of species form cooperative alliances for the purpose of reproduction. Such alliances may increase an individual's success in aggressive interactions with other males (baboons, *Papio cynocephalus*: Bercovitch 1988; lions, *Panthera leo*: Grinnell et al. 1995), increase his success in mate guarding (dolphins, *Tursiops* sp.: Connor et al. 1992) or increase his attractiveness to females (ruffs, *Philomachus pugnax*: Van Rhijn 1973; long-tailed manakins, *Chiroxiphia linearis*: McDonald 1989b). Cooperative alliances can be highly variable in size, duration and

prevalence, even within a single population (Whitehead & Connor 2005).

Two major hypotheses explain within-population variation in male alliances. Variation could reflect fixed strategies adopted by individuals and held constant throughout that individual's lifetime (Feh 1999). Alternatively, variation in alliances could reflect dynamic switching between alliance types by individual males to improve their expected reproductive success (Noë 1994). When individuals change alliance tactics, these changes may reflect differences in male quality or condition, age or ecological conditions.

The questions of how and why alliances vary are of interest for several reasons. Variation in alliances may reflect differences in the costs and benefits of helping (or receiving help) between individuals, which is, in turn, of interest in answering the question of why individuals

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cooperate. Furthermore, theoretical modelling has shown that variation in behaviour may be a stabilizing force in the evolution of cooperation (Fishman et al. 2001; McNamara et al. 2004). However, empirical evidence of the extent and source of variation in male alliances is scarce. I investigated social organization and variation in cooperative alliances in the lance-tailed manakin, *Chiroxiphia lanceolata*, with the goal of understanding how and why male alliance types vary. Specifically, I characterized male alliances and investigated whether variation arises from fixed strategies or dynamic switching between alliance types.

Male lance-tailed manakins form alliances and cooperate to attract females in a lek mating system, similar to other *Chiroxiphia* manakins (Snow 1963; Foster 1977, 1981). Cooperation by the subordinate 'beta' males of these partnerships is thought to be necessary for the dominant 'alphas' to reproduce, and necessary for betas to achieve alpha status (Foster 1977; McDonald & Potts 1994). Long-term associations between males may improve coordination and therefore success in attracting females (Trainer & McDonald 1995; Trainer et al. 2002). Alliances of congeneric long-tailed manakins are known to vary in the number of individuals that perform paired displays for females, but all territorial males apparently form partnerships and display cooperatively for females (Foster 1977; McDonald 1989a). In my study population of lance-tailed manakins, social organization ranges from solitary alpha males to alliances of up to four males that display in pairs for females at the same display area.

The assessment of individual status for all males present at display areas is a prerequisite for investigating alliances. However, assessment of individual status in lance-tailed manakins is complicated by the large number of males that may interact at one display area and the fact that aggressive interactions are rare and difficult to observe. Studies of congeneric manakins have either defined alphas as those males observed copulating (Foster 1977) or have defined a set of criteria that alpha or beta males must meet (McDonald 1989a). The former approach precludes assessment of the reproductive success of subordinate males, a key issue in the evolution of cooperative behaviour, as males that copulate while betas would be defined as alphas. The second approach is difficult to apply when the behaviours of interest are rare, and may decrease the ability of observers to detect variation in male alliances. For example, unsuccessful alpha males may never perform complete displays for females, making it impossible to identify their partners based on display elements that occur only in advanced courtship displays. A reliable but sometimes elusive indicator of male status in *Chiroxiphia* manakins is the observation of multimale displays for females that progress to solo displays (Foster 1977; McDonald 1989a). Such displays are not always followed by copulation, and participation unambiguously identifies both the alpha and beta individuals of a displaying pair: the beta leaves before courtship is complete while the alpha continues solo display. In this study, I used these multimale displays for females that progress to solo displays to identify 'known-status' pairs, and then developed a method to identify alpha and beta status

independent of actual copulations and that is robust to situations where not all behaviours of interest are observed.

If variation in alliance type results from fixed strategies, individual alpha males are predicted to remain in the same alliance types within and between years. Alternatively, if variation reflects dynamic changes in individual alliance tactics, individuals are predicted to vary in the types and strength of alliances in which they participate throughout their alpha tenure. I characterized alliances of male lance-tailed manakins and determined the frequency of variation in these alliances within the study population. I tracked individual alphas across multiple years to determine whether the observed variation results from fixed strategies or dynamic alliance changes. Finally, I considered the influence of two possible sources of variation in male alliances by examining changes in alliances in relation to males' age and alliance history.

METHODS

Study Species

The lance-tailed manakin is a small (ca. 15.5–22 g), mostly frugivorous bird in the family Pipridae. Courtship behaviour of lance-tailed manakins includes both song and dance displays. Songs are duets sung in synchrony by two males positioned on a high perch. Dance displays consist of up to 11 display elements, including two-male and solitary components (DuVal 2005a). Male partners display for females on 'display areas', which encompass 525–4500 m², with approximately one display area per 1.1 ha of uncleared land on the study site. Display areas include one to four display perches where one alpha and his partner(s) perform dance displays. The spatial arrangement of display areas is consistent with that of an exploded lek (Bradbury 1981). Females move between display areas to observe courtship displays. They rear their chicks without male assistance. Male lance-tailed manakins pass through a series of three distinct plumage stages before attaining definitive adult plumage in their fourth year (DuVal 2005b), and only males in adult plumage perform courtship displays for females (DuVal 2005a). In addition to those males that display for females, multiple adult and subadult males are regularly present at display areas and interact in duet songs and dance displays when females are not present.

Study Site and General Methods

I conducted fieldwork on a 46-ha plot at the eastern tip of Isla Boca Brava, Chiriquí Province, Panamá (8°12' N, 82°12' W). The habitat on this site is mostly secondary growth, dry tropical forest dominated by species of Euphorbiaceae, Melastomataceae and Myrtaceae, with a few remnant old growth trees in low marshy areas. The terrain includes several steep gullies and seasonal streambeds. The study population of lance-tailed manakins is resident year round at this site. Nesting and courtship begin in late March and usually continue at least until early July (DuVal 2005a) and possibly as late as September (Wetmore 1972).

I conducted fieldwork for a total of 16.5 months from July 1999 to May 2004, with the majority of captures and observations occurring during March–June in 2000–2002.

Lance-tailed manakins were captured with mist nets, individually marked with a unique combination of one numbered aluminium and three coloured plastic leg bands, and released at the site of capture. Between 1999 and 2004, 457 postfledging individuals were captured during a total of 2155 mist net-hours (one 12 m net open for 1 h), and 132 additional individuals were banded before fledging. All field techniques were approved by the Animal Care and Use Committee of the University of California, Berkeley, and by the Autoridad Nacional del Ambiente, Panamá.

Absolute age of individuals was determined by capture in any of the predefinitive male plumages (DuVal 2005b). Males first captured in definitive plumage were classified as fourth year or older in that year, allowing assessment of the relative age of display partners when the minimum age of one partner exceeded the absolute age of the other.

To avoid potential biases that could be introduced by the distribution and colour of colour bands, two bands were applied to each leg, and band combinations were chosen semirandomly (i.e. researcher discretion was exercised to ensure that birds banded in the same area were not overly similar). The distribution of band colours among males of different status classes was not significantly different from expectation based on their frequency in the population ($\chi^2_2 < 5.99$, NS for each of the 11 band colours, $N = 34$ alphas, 28 betas and 64 nonpair individuals).

Behavioural Observations

Behavioural observations were conducted at 16–28 display areas per year, with a subset of 12–18 core display areas observed two to three times per week. A total of 4146 h of behavioural observation were conducted from 2000 to 2004. Males were active on display areas throughout each field season. Standard observations consisted of 2-h sessions of all-occurrence sampling at one display area (Altmann 1974), although 30-min and 1-h sessions were conducted in 2003 and 2004. During observation sessions, observers recorded the identities of all individuals present in each 5-min period, the plumage phase of all observed birds (which served as a cross-check to colour band reading), and the occurrence and duration of individual and pair behaviours. In particular, observers recorded the identities of males (1) singing duet songs together, (2) displaying for females, (3) performing solo or paired pip flights (see below), and (4) chasing or displacing other males. The schedule of observations for different display areas was predetermined to ensure that display areas were observed evenly throughout the field season and that all areas were observed at a range of times of day, with no bias towards display areas that were particularly active at the start of each observation session. Two to four researchers conducted observations in each year, and observation duties were rotated systematically to control for observer bias at any one display area.

Analyses of male status were limited to display areas that were observed for at least 10 observation sessions, and considered only observations of individuals for which complete colour band combinations were recorded. I defined males as ‘affiliated’ with a given display area if they performed paired displays (duet songs or dances) on that display area (following McDonald 1989a).

Description of Key Displays

Male displays and the courtship sequence are described elsewhere (DuVal 2005a), but here I summarize three display behaviours that are particularly critical in defining male status: duet songs, pip flights and eek displays. Duets are closely overlapping songs phonetically resembling the phrase ‘que rico’ and given by two males perched approximately 10 cm apart, usually in a high tree. Pip flights are generalized mate attraction displays that centre on the display area, in which one or two males fly between high perches, giving a pip call each time they land (about every 5 s). Eek displays occur at the end of bouts of leapfrog dancing. In these displays, one male turns to the other and gives a sharp, metallic vocalization, rapidly jumping from the display perch in an arc and flying to nearby vegetation. Dance displays were scored as being ‘for females’ only when a female was present on the display perch during the dance. In this situation, males are in extremely close proximity to the female (ca. 5 cm at nearest approach) and the directionality of the display is unambiguous. A dancing bout was considered to have ended when the target female left the display perch and the males discontinued courtship display.

Paired Male Interactions

I measured the following behavioural variables for all male pairs: number of two-male dance displays performed for females per h, two-male pip flight displays per h, number of paired displays with no female present performed per h, and a ‘simple ratio’ association index estimating strength of association between two individuals for duet singing (Ginsberg & Young 1992). This association index was based on the number of observation sessions during which individuals were observed interacting with each other in duet songs and was calculated as follows:

$$AI = (\text{Sessions A \& B}) / ([\text{Sessions A \& B}] + [\text{Sessions A \& other}] + [\text{Sessions B \& other}])$$

where ‘&’ indicates partnering for a bout of duet singing and where A is one male partner and B is the second. Association strength was analysed by using the number of observation sessions in which males interacted rather than the number of individual display bouts because birds interacting during one session often did so for multiple duetting bouts. In addition, sessions at the same display area occurred on different days and were regularly spaced throughout the field season, and therefore represent relatively independent samples of pair affiliation. I limited

the association index analyses to pairs in which the interacting individuals were involved in a total of five or more duetting bouts in that field season to avoid inflating the AI values of rarely observed males.

Individual Behavioural Variables

I measured the following aspects of behaviour for individual males: proportion of observation sessions during which an individual was observed, solo pip flight displays per h, displays for females per h during which a male performed the eek display, and solos for females per h with and without preceding two-male displays.

Dominance at Known-Status Sites

Male status was defined by the observation of paired displays for females that progressed to solo displays. Alpha individuals were those males that remained to continue solo display for the female, whereas beta individuals were males that left the display area although the female remained on the display perch and display continued. This behavioural cue has been identified as a reliable status indicator in other *Chiroxiphia* manakins (Foster 1977; McDonald 1989a). Because the majority of displays did not end in copulation, the occurrence of solo display is distinct from copulatory success. Displays for females that include a paired followed by a solo component are particularly informative of male status for three reasons. First, these displays involve both the alpha and beta individuals: purely solo displays might reflect the absence of one or the other male rather than the status of the displaying individual. Second, they involve conspicuous and noisy behaviours that would alert dominant males to the display's occurrence should 'cheaters' perform them on another male's display area. Finally, paired displays that progress to solo displays are neither necessary nor sufficient for copulation to occur: females also copulate after entirely solo displays, and the majority of all displays end when the female leaves without copulating.

I identified a subset of display areas where the alpha and beta male were known via observation of these paired followed by solo displays. Additional males present on these display areas were categorized as 'nonpair' males. I then compared the behaviour of identified alpha and beta males with that of nonpair individuals in the area to identify behavioural correlates of male status.

Dominance at Unknown-status Sites

I combined variables related to status in 'known' pairs using a principal components analysis followed by logistic regression as described below, with the goal of developing a model for status that could be applied to display areas where paired followed by solo displays were not observed. When alpha–beta status was identified as 'known' for the same pair of males in multiple years, I randomly selected 1 year of data to include in this analysis.

The behaviour of both individuals participating in a paired display is similar, and there is little if any aggressive interaction between partners (personal observation). Because of this, the alpha and beta males within an identified pair are indistinguishable without individual-based information. Therefore to identify the alpha male, I assessed status in a nested fashion: pair behavioural variables were compared to identify the alpha–beta pair, and then individual behavioural variables were assessed separately to identify alpha individuals. This technique also allowed alpha males to be identified when no beta was present.

Statistical Analysis

I accounted for differences in observation times between display areas by calculating rates of behaviours within each field season. Social organization was assessed by using data from all display area-years at which male status could be identified. The effect of status on affiliation patterns was analysed by using penalized quasiliikelihood generalized linear mixed models (GLMM) in R 2.3.0, with a Poisson error distribution and individual identity as a random effect (Breslow & Clayton 1993).

Because dependent variables were not normally distributed, I used nonparametric tests to compare the behaviour of males of different status categories. Behavioural variables relating to status were highly correlated with each other so I combined them in a principal components analysis, using a correlation matrix to standardize the variables. I then used a logistic regression of the first and second principal components on status to create a predictive logistic regression for application to unknown pairs. The regression model was simplified by backwards elimination and likelihood ratio comparison between full and restricted models (with $P < 0.05$ indicating that the variable made a significant contribution to the model and hence should be retained). I tested the accuracy of the resulting model by using leave-one-out cross-validation (Molinaro et al. 2005) conducted in the statistical package R (Ihaka & Gentleman 1996). The same procedures were used to create a model defining alpha status of individual males.

The equations for probability of alpha–beta pair status and individual alpha status were applied to all interacting pairs and all adult-plumage males observed at display areas to identify the alpha and beta males in each area. Pairs of males were designated as alpha–beta if they had a high calculated probability of alpha–beta status (greater than 0.75) while all other pairs at that display area had a low probability of alpha–beta status (< 0.5). I examined in detail cases where no pair or more than one pair had a high probability of alpha–beta status to determine whether they reflected real associations of males or were an artefact of the model. In cases where two males partnered for multiple displays for females but had low AI values because of high levels of interaction at other display areas, I considered these males to be partners.

Within each identified alpha–beta pair, the alpha individual was the male with the higher calculated

probability of alpha status relative to his partner. When no pair was identified as alpha–beta, an alpha was still identified when one individual at a given display area had an assessed probability of alpha status greater than 0.90.

Means are presented \pm SD. All statistical tests were performed in the program JMP 5.0 (SAS Institute Inc., Cary, NC, U.S.A.) unless otherwise noted.

RESULTS

Correlates of Alpha and Beta Status

I identified alpha and beta status in 16 distinct pairs of males ($N = 16$ display area-years) using the criterion of paired male displays for females followed immediately by solo displays by one of the males. At each display area where the alpha–beta pair was known, there were three to nine pairs of males that participated in duet songs; these individuals were considered below in identifying the behavioural correlates of male status ($N = 73$ total pairs, 125 individuals).

When compared to other pairs of interacting males, the alpha–beta pair (1) had significantly higher values of the duetting association index, (2) performed the vast majority of paired pip flights, (3) performed the majority of dance displays for females, and (4) performed the majority of dance displays when no females were present (two-tailed) Kruskal–Wallis tests: $\chi^2_1 > 3.37$, $N = 16$ alpha–beta pairs and 57 other pairs, $P < 0.001$ for all comparisons; Fig. 1a).

Behaviour of alpha individuals differed from that of beta and nonpair individuals present on the display area in several respects. Alpha males (1) were present for a significantly greater proportion of observation sessions at each display area, (2) performed the vast majority of solo male displays for females, (3) performed the majority of solo pip flights, and (4) were the only males to give the eek vocalization during displays when females were present (Kruskal–Wallis tests: $\chi^2_2 > 35.20$, $P < 0.001$ for all comparisons; Fig. 1b).

Predictive modelling of pair status

All behavioural measures loaded positively on the first principal component of the pair behavioural variables (PC1), while two-male displays for females had the highest loading in the second principal component (PC2; Table 1). The variable ‘two-male displays without females’ was excluded from this analysis because it appeared to be highly variable among display areas where male status was not known, and was therefore not a reliable indicator of status despite the strong correlation at the assessed display areas with males of known status.

PC1 and PC2 strongly predicted status among known-status pairs (logistic regression: $\chi^2_1 > 64.58$, $R^2 = 0.84$, $P < 0.001$; Fig. 2a). The influence of PC2 was comparatively slight ($P = 0.10$ in the full model), but removing this variable resulted in a significant decrease in explanatory power for the restricted model (maximum likelihood test: $P < 0.05$) and so PC2 was included in the final model. Leave-one-out cross-validation showed that the average

success of the model in predicting pair status in test data sets was 95.8%, indicating that the model was an accurate predictor of status in known-status pairs ($N = 73$ pairs).

I calculated the probability of alpha–beta status for interacting pairs observed in 47 display area-years in which two-male followed by one-male displays were not observed ($N = 201$ male pair-years). One clear alpha–beta pair was present in 36 display area-years ($P_{(\text{alpha–beta})} > 0.95$ for only one pair in each of 32 display areas; $P_{(\text{alpha–beta})}$ between 0.76 and 0.90 for only one pair in each of four additional display areas). In four display area-years there was no apparent alpha–beta pair ($P_{(\text{alpha–beta})} < 0.18$ for all tested pairs in that area). In five areas, two pairs had $P_{(\text{alpha–beta})} > 0.5$, reflecting multiple high-ranking pairs present at the same display area (see below). In the remaining two areas, pair interactions were rare enough that pair-based assessment of status was not possible, but the areas were still considered in individual status tests.

Statistical outcomes agreed with observers’ subjective assessments of male status made in the field with one exception: a display area statistically classified as having one alpha–beta pair was also attended by a third male that displayed for females and duetted with the alpha. This male showed a strong affiliation with an alpha at a different display area, resulting in low duetting AI values with the first alpha. I therefore classified this male as beta at both display areas and defined the area in question as having an alliance of multiple males.

Predictive modelling of individuals’ status

All behavioural measures examined loaded positively on PC1 of the individual behavioural variables (Table 1). PC1 was a strong predictor of status (coded as a binary variable, alpha or not alpha) for known males (logistic regression: $\chi^2_1 > 65.31$, $R^2 = 0.68$, $P < 0.001$; Fig. 2b). PC2 was eliminated during model simplification. Leave-one-out cross-validation showed that the average success of the model in predicting individual status was 95.7%, indicating that the model was an accurate predictor of status for known-status individuals ($N = 125$ individuals of known status).

The individual-based evaluation identified one and only one alpha male in all 47 display area-years where status was unknown ($N = 418$ individual-years). In areas where the pair analysis indicated an alpha–beta partnership, the assessed probability of alpha status was significantly higher for one of the two members of identified alpha–beta pairs (two-tailed paired t test; mean difference in $P_{(\text{alpha})} = 0.70$ for alpha versus betas, $P < 0.001$, $N = 41$ pairs). In six areas for which no alpha–beta pair was identified, an alpha individual was none the less evident (one individual with $P_{(\text{alpha})} > 0.90$, next most likely individual had $P_{(\text{alpha})} < 0.05$; in five cases the identified alpha had $P_{(\text{alpha})} > 0.95$).

Social Organization and Alliance Structure

Social organization within display areas

There were on average 8.1 ± 3.9 adult males and 3.9 ± 1.7 predefinitive males observed at each display area ($N = 63$ display area-years). Adult males at each

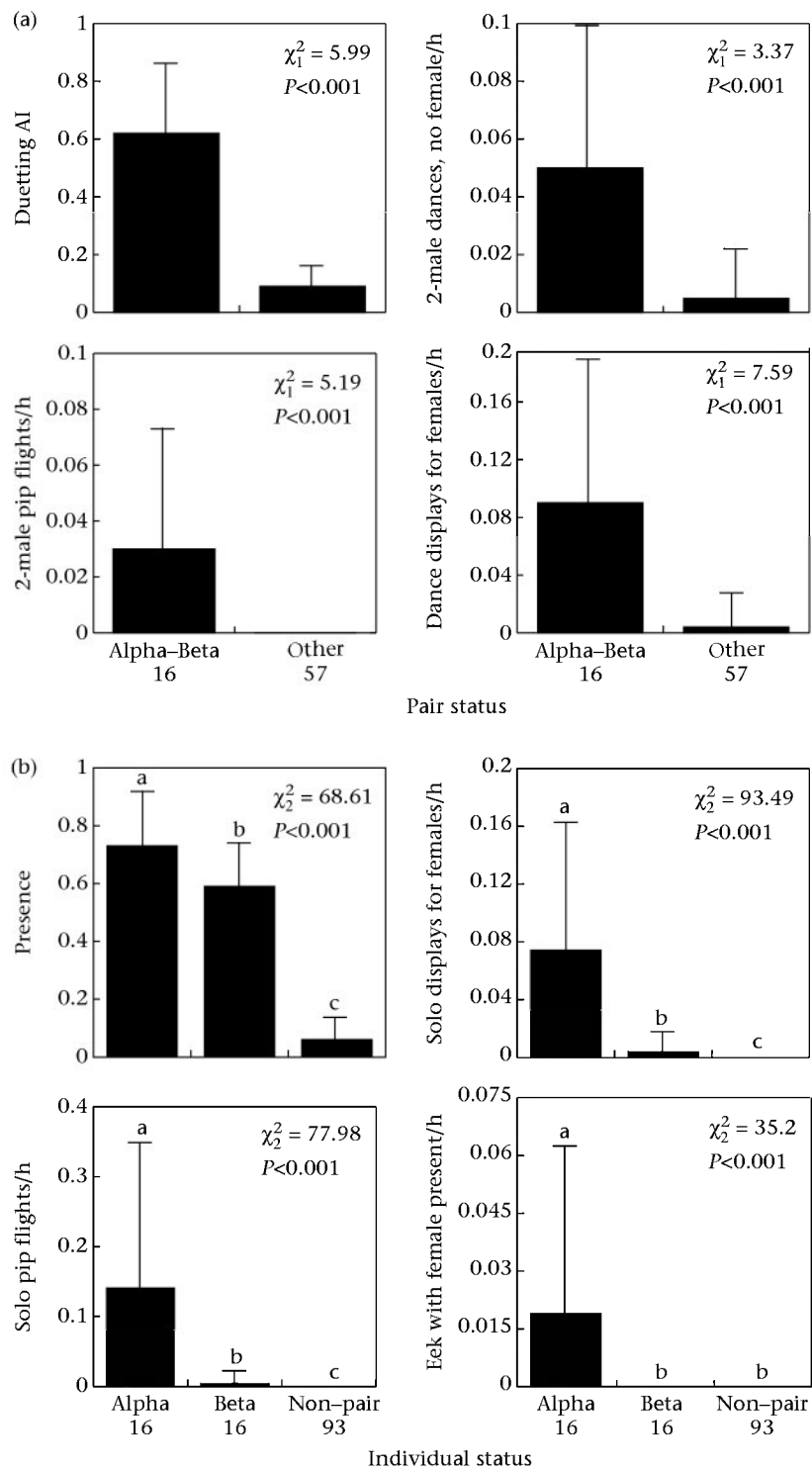


Figure 1. Behavioural differences between known-status alpha and beta individuals and other males at the same display areas. (a) Pair-based interactions and (b) individual behaviours (Kruskal–Wallis test). Means are shown \pm SD. Letter codes (a, b or c) within each graph designate groups that are significantly different from each other (two-tailed Mann–Whitney tests: $P < 0.05$). ‘Solo displays for females’ refers to any solitary courtship display for a female present on the display perch, regardless of whether it was preceded by paired male display; ‘presence’ is the proportion of observation sessions that an individual was seen in the display area; and ‘duetting AI’ is an association index measuring the duetting pair bond between two males (see Methods for calculation). ‘Dance’ refers to a two-male display involving cartwheels and slow flight displays. Dances were considered to be ‘for females’ only when the female directly attended the display by alighting on the display perch. Sample sizes are listed below status categories.

Table 1. Component loadings of behavioural variables as quantified by principal components analysis

	Pair analysis		Individual analysis
	PC1	PC2	PC1
Eigenvalue	1.95	0.68	2.54
Variance explained (%)	65.06	22.61	63.40
Cumulative variance explained	65.06	87.67	63.40
Eigenvectors			
Duetting AI	0.63	-0.10	
Two-male pip flight	0.57	-0.62	
Two-male dance for female	0.53	0.78	
Presence			0.48
Solo pip flight/h			0.53
Solo for female/h			0.55
Eek in displays/h			0.43

$N = 73$ pairs in 16 display area-years in the paired analysis; $N = 125$ individuals in the individual analysis. Duetting AI is the duetting association index (see *Methods* for calculation details). 'Eek in displays' refer to the performance of the eek call during a display when a female was present on the display perch. 'Presence' was defined as the proportion of the total observation sessions conducted at one display area-year 1 during which a given male was recorded as present.

display area included one alpha male and an average of 1.0 ± 0.5 beta and 6.2 ± 3.7 nonpair males ($N = 63$ display area-years). As many as 15 pairs of males engaged in duet songs and dance displays performed when no females were present (4.5 ± 2.5 pairs, $N = 63$ display area-years). However, only alpha–beta pairs performed dance displays for females ($N = 195$ displays for females). The vast majority of adult males observed on the study site were neither alphas nor betas: a total of 73.7 ± 18.6 nonpair adult males were present at observed display areas in each year of the study, compared to 30.7 ± 5.8 males that were alpha or beta in each year ($N = 4$ years).

Status was significantly related to the number of display areas at which a male was observed or with which a male affiliated (GLMM: observation: $F_{2,97} = 11.4$, $P < 0.001$; affiliation: $F_{2,97} = 6.48$, $P = 0.002$, Fig. 3a, b). Alpha males typically affiliated with only one display area (mean = 1.1 ± 0.3 display areas, $N = 63$ male-years). Males that were not alphas were affiliated with more display areas than alpha males (GLMM model contrasts: alphas compared to betas: $t_{1,97} = 3.52$, $P < 0.001$; alphas compared to nonpair males: $t_{1,97} = 2.73$, $P = 0.008$; betas compared to nonpair males: $t_{1,97} = 1.17$, $P = 0.24$). Status was also related to the number of partners with which a male sang duet songs (GLMM: $F_{2,97} = 29.69$, $P < 0.001$; Fig. 3c). The alpha male at each display area engaged in vocal duets with significantly more partners than did males of any other status (GLMM model contrasts: alphas compared to betas $t_{1,97} = -4.50$, $P < 0.001$; alphas compared to nonpair males: $t_{1,97} = 7.52$, $P < 0.001$; betas compared to nonpair males: $t_{1,97} = 2.34$, $P = 0.02$).

Age and status

In partnerships where the relative age of the alpha and beta was known, alphas were older than betas in 11 of

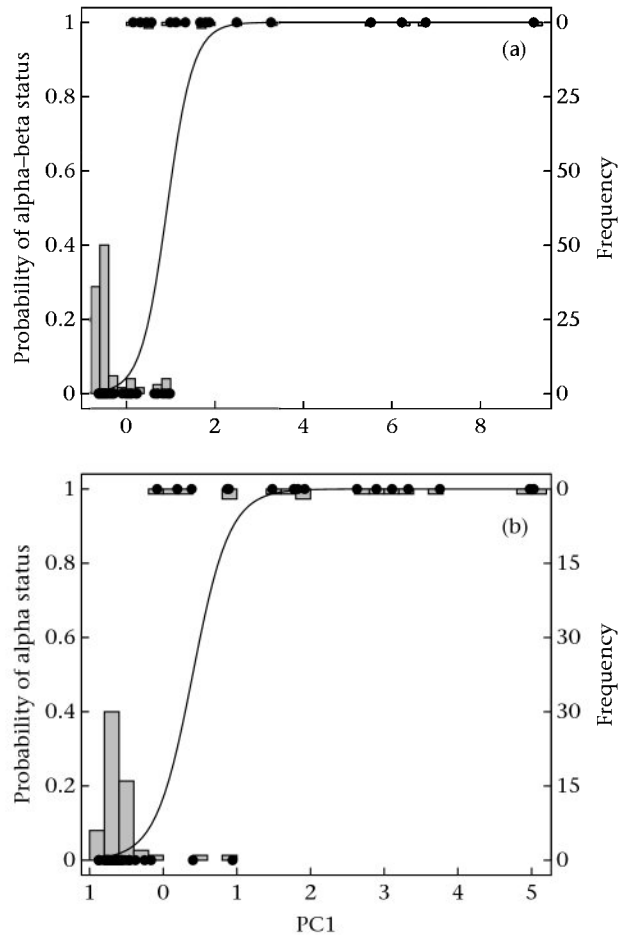


Figure 2. The first principal component, PC1, in relation to status for (a) pair and (b) individual behavioural variables among males present at display perches where male status was known. (a) Logistic regression of only PC1, the main predictor of status, is shown because PC2 contributed little to the model. The final model also included PC2 (logistic regression: pairs: $\chi^2_1 = 64.58$, $P < 0.001$; individuals: $\chi^2_1 = 65.31$, $P < 0.001$). Points at the top of the graphs correspond to the PC1 of behavioural variables of (a) known alpha–beta pairs or (b) known alpha individuals at a given display area; points at the bottom of the graphs indicate (a) interacting male pairs that were not alpha–beta pairs and (b) individuals that were not alphas at the same display areas. The observed data are presented in frequency histograms with the associated scale on the right-hand axis (following Smart et al. 2004).

12 pairs (91.7%; binomial test: hypothesized probability = 0.5, $P = 0.002$). All alpha and beta males were in definitive adult plumage (i.e. fourth year or older). Three alpha males were known to be in their eighth year or older, and one alpha was at least in his ninth year. Males of known age that became betas were generally younger than males of known age that became alphas (Fig. 4). However, betas were not necessarily young males: one male was known to be in his ninth year or older when he first became a beta. Known ages of nonpair adults ranged from the fourth to the eighth year, spanning the full range of detectable known ages of adults given plumage stages and banding history at the study site. Six nonterritorial males were in their eighth year or older. This suggests that while alpha males

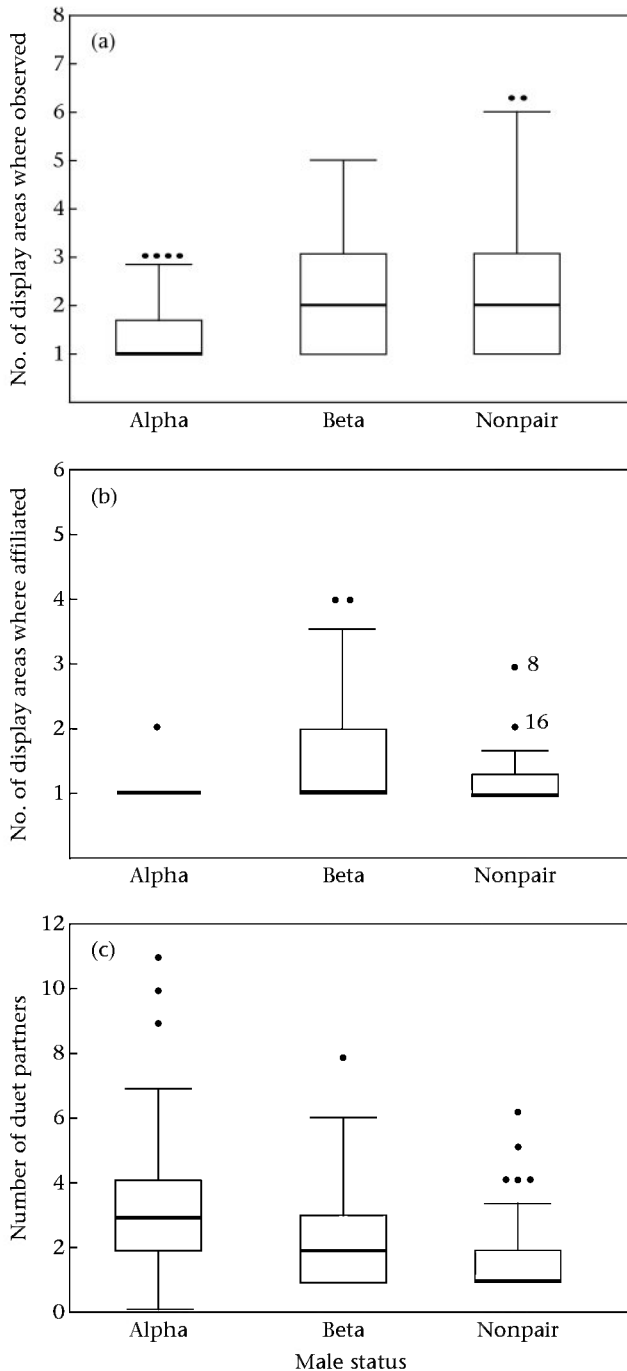


Figure 3. Spatial alliances and number of duetting partners in relation to males' status. (a) Observations of males at and (b) affiliations with display areas. Affiliation was defined by duet singing observed at a given display area. (c) Number of duet partners. See text for statistical comparisons. $N = 63$ alpha, 59 beta and 98 nonpair male-years for all comparisons. Horizontal line indicates the median and the box surrounds the 25% and 75% intervals of the data. Vertical lines show data within 1.5 interquartile ranges of this interval, with points marking data outside this range (sample size of outliers indicated for nonpair males in b).

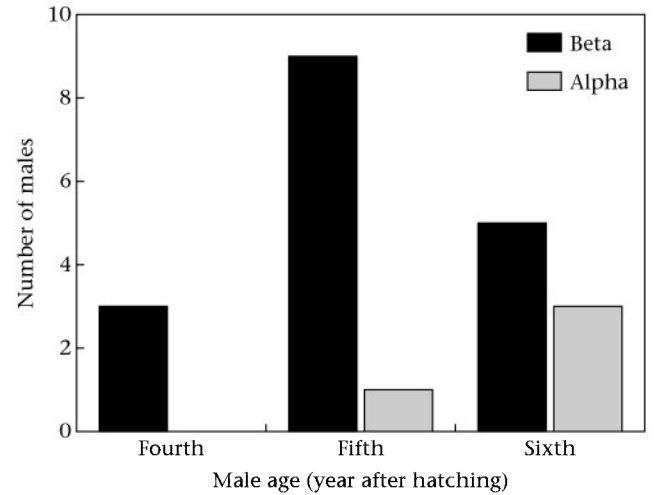


Figure 4. Known ages of alpha and beta males in their first year of tenure. $N = 17$ betas, 4 alphas. Age was determined by prior capture in a predefinitive plumage.

tend to be older than their beta partners, age is not an absolute predictor of individual status.

Variation in alliances by alphas

Single alliances: one alpha and one beta individual. Typically, each display area was occupied by one alpha and one beta male (79.4% of 63 display area-years), and only that pair performed dance displays for females. Within these single alliances, there was considerable variation in AI between alpha and beta partners (mean AI = 0.59 ± 0.21 , range 0.1–1.0, $N = 50$ pairs), suggesting that there was a range of partnership intensities within the population.

Association strength did not increase when partnerships remained intact for more than one breeding season (mean difference in duetting AI of first and second years observed = 0.13 ± 0.39 ; two-tailed Wilcoxon signed-ranks tests: $T = 0.34$, $N = 9$, $P = 0.30$).

Multiple alliances by one alpha. Some alliances at a single display area included more than two individuals in the same breeding season (11.1% of 63 display area-years, $N = 15$ male pairs). In all cases these pairs consisted of one alpha male partnered with multiple subordinates. Six of these alphas had two partners each and one had three high-ranking partners. Alliances with multiple betas resulted either from temporal changes in partnerships (one beta being replaced by another, $N = 3$ display area-years), or from the simultaneous presence of multiple beta partners ($N = 4$ display area-years). There was no discernible dominance hierarchy among beta males at the same display area, as they rarely if ever interacted with each other.

No alliance: alphas without beta partners. Some alpha males had no apparent beta partner (9.5% of 63 display area-years). In each of these cases, there was one clear alpha that performed duet songs with several other adult males (range 2–10 duetting partners) but did not have

strong affiliations with any of them. Five of these alphas had beta partners before ($N = 1$ alpha) or after ($N = 4$ alphas) holding solitary alpha status, while one was never observed forming an alliance with a subordinate male. In one case, an alpha held the same territory for 2 consecutive years without establishing a strong affiliation with a beta, although he did so in later years.

Alliance Type and Courtship Display

Males of all alliance types were observed performing courtship displays for females that perched on their display perches. Power was insufficient to allow a test for differences in the rate of female visits to alliances of different types (Kruskal–Wallis test: $B = 0.09$, $\alpha = 0.05$).

Alliance Duration

Alliances were usually long-term associations of individuals. Many alliances were formed before the present study began or continued past its end, precluding an accurate estimate of the duration of most alpha–beta partnerships. However, 17 of 37 (46%) partnerships persisted for two or more breeding seasons. The shortest observed alpha–beta associations lasted for 1 month ($N = 2$), and the longest persisted for at least four breeding seasons ($N = 2$).

Individual alpha males were observed to change alliance types over time. Males observed from the start of their alpha tenure seemed to converge to a single alliance over time, even though their specific partners sometimes changed (Fig. 5a). Changes in alliance type also occurred in alpha males that had been alphas for longer periods (Fig. 5b).

Variation in Alliances by Betas

The majority of betas were allied with only one display area and with only one alpha male, despite being observed at other display areas more often than their alpha partners. Unexpectedly, three males that were beta at one display area simultaneously held alpha status at another area. In each case these males had a history of prior beta status at the area where they were still betas. Furthermore, territories where these males were alpha were not previously used as display areas and shared a common boundary with territories where they held beta status, suggesting that maintaining dual alpha–beta status was a way of ‘budding’ off of their alpha partner’s territory. In addition, one male was simultaneously beta at two different display areas and with two different alpha partners. This male flew between display areas multiple times each day, and associated with a different group of males in each area.

DISCUSSION

The complex and varied social behaviour of lance-tailed manakins is characterized by long-term cooperative

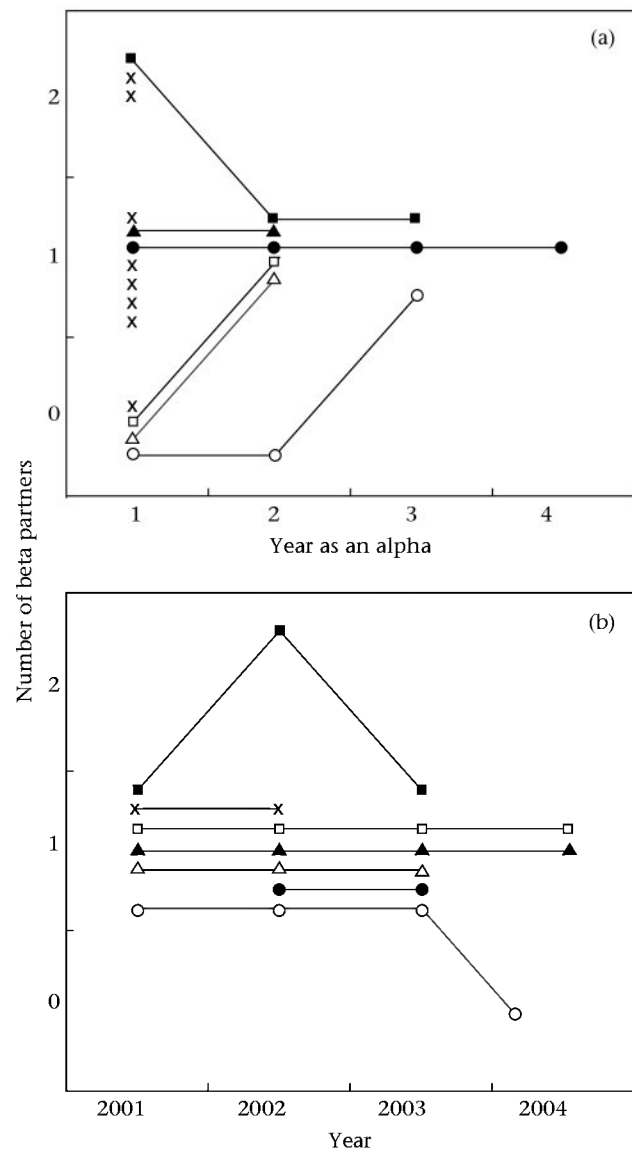


Figure 5. Changes in alliance types of individual alphas over time. Connected lines represent individual males followed through several years of their alpha tenure. Number of beta partners indicates the alpha’s alliance type: alphas with no beta partners were solitary alphas and those with two betas were alphas with multiple alliances. (a) Alpha males observed from their first year of alpha tenure. X’s without connecting lines represent the alliance types of seven alphas observed in only the first year of their alpha tenure. (b) Alpha males of unknown tenure observed in multiple years.

alliances between adult males and the presence of multiple adult and predefinitive males at display areas. Alpha and beta males are distinguished from other males by clear affiliative behaviours that occur regardless of whether females are present.

Male alliances were most commonly one alpha male partnered with one beta male. However, the degree of association between alpha and beta partners varied from extremely close affiliations in which the alpha–beta pair associated almost exclusively with each other, to multi-male associations where one alpha displayed with multiple subordinate males. One clear alpha male could be

identified at every display area, but I unexpectedly detected several display areas in which the alpha male had no apparent beta partner, but still performed courtship displays for females. This notably contradicts the generalization that *Chiroxiphia* manakins are 'obligate' cooperators (Trainer & McDonald 1993). Assuming that cooperation is an invariant aspect of *Chiroxiphia* manakins underestimates the role of selection on individual behaviour in this system. The range of affiliations reported among male lance-tailed manakins is consistent with variability in male alliances reported in other species with male–male cooperation (Packer et al. 1991; Krützen et al. 2004; Krakauer 2005).

Variation in association types can come from either fixed long-term strategies held by individuals (e.g. horses, *Equus caballus*: Feh 1999) or from dynamic shifts in individual alliance tactics (e.g. chimpanzees, *Pan troglodytes*: Nishida 1983). My study has shown that individual alpha males may form different types of alliances throughout their alpha tenure. We can thus reject the hypothesis that variability in alliance types reflects fixed strategies by individuals.

Changes in alliance types within the lifetime of an individual raise the question of what influences individual alliance decisions. Alliance decisions may reflect changes relating to individual age, quality, availability of display partners or an interaction of these factors. My sample size of known-age males in different alliance types is too small to assess whether age influences alliance structure, but two facts argue against a strong direct relation between age and alliance type: (1) males began alpha tenure at a variety of ages, and (2) males that had been alpha for several years still changed alliance types. Variation in alliances seemed to result from changes in experience level or available partners rather than absolute age. The tendency to move towards alliances with a single beta partner suggests that solitary alphas display singly because they lack a suitable partner, not because high relative quality allows them to attract females without the assistance of other males. Similarly, alphas with multiple betas appeared to be in the process of selecting from several suitable subordinate partners. Perturbations such as the loss of a partner also resulted in experienced alphas forming multimale alliances or displaying solitarily for up to a full breeding season, suggesting that forming a suitable partnership can be difficult even for experienced males. Observed changes in an individual's alliances over time suggest that a dynamic switching model of alliance formation may be appropriate for this system (Whitehead & Connor 2005).

The behaviour of beta-ranked males was more variable than that of alphas. Betas often attended multiple display areas, and their movements between areas were independent of their alpha partner. Of particular interest is the observation of several beta males that maintained beta status at one display area while behaving as alpha males at an adjacent area. This behaviour suggests that participation in alliances may benefit subordinates in ways other than linear queuing. Cooperative displays by these 'budding' males and their previous alpha partners may reflect bet hedging by the budding individuals (allowing

them to maintain their former positions should the new display areas fail) or mutual benefits obtained from continued joint displays. Such behaviour may also carry costs from increased exposure to predators or increased energy expenditure as the beta travels repeatedly between display areas. This study focused on variability in alliance types, but did not address changes in partnerships that do not result in changes in alliance structure. Future analysis of partnership changes by individual betas will be informative in assessing the relative importance of this budding behaviour compared to other potential ways of attaining alpha status, such as queuing within a social group.

Investigating how and why alliances vary is of particular importance in interpreting individual decisions to cooperate. The dynamics of how partnerships are formed remain uncertain, although alliance formation appears to be an active and dynamic search on the part of both the alpha and beta male. I detected no evidence of affiliations among lower-ranking individuals, suggesting that coalitions are not formed for the purpose of 'overthrowing' existing alpha–beta partnerships but rather that males attain high status independently and then solidify a display partnership. The variability of male association types reported here suggests that alpha males may form stable alliances in a variety of ways. Future investigations should therefore consider whether individual quality or condition affects the types of alliances that males can join, and whether variability in alliance types affects the fitness benefits for either member. Males that form alliances by selecting from among multiple subordinates may attain a better 'fit' than males that start their alpha tenure as solitary alphas and then attract a beta over time, which may result in increased success in attracting females. Of particular interest is the effect of alliance structure and changes in alliances on the mating success of the allied males. Long-term behavioural data from the study population will allow the comparison of the realized reproductive success of individuals with different alliance histories.

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