

NO EVIDENCE OF FEMALE CHOICE FOR A CONDITION-DEPENDENT TRAIT IN THE AGAMID LIZARD, *CTENOPHORUS ORNATUS*

by

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Summary

Female choice has rarely been documented in reptiles. In this study we examined the variation, condition-dependence and female preference for a range of male morphological and colour traits in the agamid lizard, *Ctenophorus ornatus*. Colour traits were measured with reflectance spectrophotometry which allows the accurate quantification of colour traits independent of the human visual system. All the colour traits varied greatly in brightness but only the throat showed high variation in the spectral shape. For the morphological traits, chest patch size showed the highest amount of variation and was also condition-dependent. Males with a larger chest patch also had a patch which was a darker black. Female mate choice trials were conducted on male chest patch size and body size, which is the trait females have preferred in other lizard species. Females showed no preference, measured as spatial association, for larger males or males with bigger chest patches. In post-hoc tests females did not prefer males with brighter throats or darker chests. Our findings suggest that females show no spatial discrimination between males on the basis of a range of traits most expected to influence female choice.

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Introduction

Female mate choice has been well documented in many taxa (Andersson, 1994), however in reptiles female choice appears to be rare (Tokarz, 1995; Olsson & Madsen, 1998). There are only two species of lizards in which female mate choice has been conclusively demonstrated. Both of these species showed female choice of male body size (Cooper & Vitt, 1993; Censky, 1997). The paucity of female choice is especially surprising as lizards are often sexually dimorphic, frequently have extravagant traits and numerous species have polygynous mating systems (Stamps, 1983). However, many investigations of female choice in lizards are based on field studies in which it is difficult to disentangle the effects of intra and inter-sexual selection (Olsson & Madsen, 1998).

Male traits subject to intra-sexual selection have frequently been found in lizards (review see Olsson & Madsen, 1998). Body size, head size and various types of body coloration have all been found to influence male contest success (Olsson & Madsen, 1998; Martín & Forsman, 1998). In territorial lizards male contests frequently determine territory size and quality. Consequently identifying female choice of male traits in lizards is difficult as female choice of a male's traits has to be distinguished from choice of male 'resources' (e.g. territory quality). Moreover, females may pay attention to both a male's resources and the trait which determined the resource acquisition (Qvarnstrom & Forsgren, 1998). However, Hews (1990) found in *Uta palmeri* that when male territory variables were controlled for there was no effect of female choice on male traits. Female choice can also act on different traits to those which determine male contest success (Qvarnstrom & Forsgren, 1998). Female choice of different traits to those involved in male contests may allow females to refine their choice amongst males who have won territories. Thus female choice may be on traits unrelated to male contest success or those also subject to intra-sexual selection.

Many lizard species have bright coloration, which is often emphasised during behavioural displays (Cooper & Greenberg, 1992). Few studies have investigated the role of colour in lizard mate choice (but see Olsson &

Madsen, 1995), though colour has been found to be important in male contests (Thompson & Moore, 1991; Olsson, 1994). However, there are difficulties in measuring colour, as our visual system and that of the species in question are not necessarily equivalent (Bennett *et al.*, 1994). Recent studies of birds which have sexually dichromatic traits in the ultraviolet (UV), have illustrated the importance of measuring colour traits independent of our visual system (Andersson *et al.*, 1998; Hunt *et al.*, 1998). These problems are very likely to be relevant to lizards as ultraviolet sensitive photoreceptors have been found, as far as we can discern, in all the eleven species of lizards which have been examined (Fleishman *et al.*, 1993; Loew, 1994; Ellingson *et al.*, 1995; Loew *et al.*, 1996).

Ctenophorus ornatus is an agamid lizard which lives exclusively on granite outcrops in southern Western Australia. Males maintain territories exclusive of other males and which typically encompass a number of female territories. Females primarily associate with the male in whose territory she resides and opportunities for associations with other males appear limited. However, a analysis of parentage using genetic markers revealed 35% of clutches were sired by a male with no overlap of the female's territory (LeBas, 2001). It is unknown whether females 'chose' these extra-territorial partners. Nor is it known if females chose the male in whose territory she resides. A test of female associations when territory variation and male interactions are removed is required to determine the role of female choice in these mating patterns.

C. ornatus is sexually dichromatic for a range of colour traits, but most noticeably in the black chest patch of males which is absent in females (LeBas & Marshall, 2000). Visual displays are common throughout the breeding season and include a push-up display which emphasises the male's black chest patch and throat region. The throat region contrasts strongly against the granite background and is a likely signal between conspecifics (LeBas & Marshall, 2000). Males are also significantly different from females in throat ultraviolet spectral shape, which is likely to reflect a difference in chroma for this region (LeBas & Marshall, 2000).

In *C. ornatus* we have a system in which females mate with the territorial partner, but frequently also with extra-territorial males. Here we test if there is female preference for male traits and if traits reliably reflect male quality. Female preference is measured in laboratory trials as female spatial association with males; unconfounded by male interactions and territory

size. We examine the coefficients of variation of male morphological and colour traits to determine which traits had the highest variation and thus were likely to be subject to sexual selection. Colour traits were measured using reflectance spectrophotometry to ensure quantification independent of our visual system. Relationships between male traits and male condition were investigated to determine if any traits honestly signal condition. We investigated female mate choice on male body size as this is the only male trait in lizards which has been conclusively shown to be subject to female choice. We also examined female mate choice for male chest patch size.

Methods

Lizards were collected from granite outcrops on farmland near Tutanning Nature Reserve, 200 km SE of Perth, Western Australia. Details of lizard housing differed for the two mate choice experiments and are described in the methodology for those sections.

Male traits

The following morphological traits were measured for 24 male lizards: snout vent length (SVL); weight; jaw length; head width and chest patch area. Head width was measured across the middle of the tympanum. Jaw length was measured from the centre of the tympanum to the tip of the snout. Morphological traits were measured with vernier callipers to the nearest 0.01 mm and weights to the nearest 0.1 g. Chest patch size was measured by capturing a video image of the chest patch and measuring the area using the OPTIMAS image analysis system.

The spectral reflectance of male colour traits were measured with a custom-built spectroradiometer ('Sub-Spec' Andor Technology Oriel; for methodology see LeBas & Marshall, 2000). All traits were measured three times on 23 lizards for the throat, 22 for the chest; ten for the dorsal base colour and nine for the dorsal stripe. Reflectance spectra were highly repeatable (LeBas & Marshall, 2000). Reflectance spectra curves were summarised using principal components analysis (Cuthill *et al.*, 1999). As is commonly found with reflectance spectra the first principal component (PC1) was nearly perfectly correlated with mean reflectance *i.e.* brightness (Cuthill *et al.*, 1999). Hence, the term 'brightness' in this manuscript refers to the total reflectance of the colour trait *i.e.* the area under the spectral reflectance curve. The remaining principal components (PC2, PC3, *etc.*) describe differences in the shape of the spectra (Endler, 1990; Cuthill *et al.*, 1999). For descriptions of the reflectance spectra only the first and second principal components are used and will be referred to as 'brightness' and 'spectral shape' respectively.

Coefficients of variation were calculated to determine the amount of variation in male traits. As coefficients of variation are meaningless when calculated from principal components scores, the coefficients of variation for the throat and chest reflectance spectra were calculated from the mean reflectance rather than PC1. Mean reflectance was calculated by summing the percentage reflectance across all wavelengths (330-700 nm). Variation in spectral shape was determined by visual inspection of the reflectance spectra curves.

The relationships between male traits and male condition were examined to determine if any traits reliably signal the condition of the male. Condition was measured as the residuals of logbody mass on the logSVL (Jakob *et al.*, 1996; Kotiaho, 1999). The body size and weight measures for the condition index were obtained on the day of capture and hence represent true field condition. One of the males had extensive scarring on one side of the abdomen where he appeared to have been bitten. This male was consistently a significant outlier (Mahalanobis distance) in condition correlations and was removed from all condition analyses.

Female association experiments

Two experiments investigating female choice of male traits were conducted; both over the summer breeding season, firstly in 1997-98 and also 1998-99. In both experiments spatial preference was used to indicate mate choice. Females collected from the field all had developing follicles. Females lay up to three clutches a breeding season, live up to five years in the field and have been recorded in the same territory in successive years (Bradshaw, 1963, 1965; LeBas, unpubl. data). If there is only a short period of receptivity in this species and females were pre- or post-receptivity at the time of trial a females decision to associate with a particular male is relevant for approaching receptivity or future clutches.

Experiment 1: Male size

Lizards were collected early in the summer of 1997 when females had developing follicles. Lizards were housed in a controlled temperature room with a photoperiod and temperature equivalent to late spring/summer breeding conditions of 15:9 hours L:D and 28/19°C day/night. Males were housed in individual cages and were separated from females by mesh which allowed visual and olfactory, but no tactile contact with females. Females were housed in groups of two with visual and olfactory, but no tactile contact with males. Heat lamps were available for basking. Lizard diet was mealworms dusted in multivitamin and calcium powder supplemented with cockroaches, termites and crickets.

Males were paired to maximise the difference in size (mean large male group: 92.9 ± 0.83 mm; mean small male group: 88.6 ± 0.55 mm). Females were randomly assigned to male pairs with the proviso that lizards which had visual and olfactory contact prior to the trials were not tested together. Males and females were used once only. Choice trials were conducted in a three sectioned arena (Fig. 1a). The two males were placed in identical side-by-side compartments separated by a solid partition and tethered by cotton to the tail to prevent them from crossing into each others area. Males thus had no physical or visual contact with one another. Females were placed in a rectangular compartment which stretched across both males compartments and were separated from the males by a clear plastic partition until the beginning of the trials. The room temperature was 28°C and an additional lamp provided a heat source above each male's brick. Lizards were allowed one hour to acclimatise to their compartments after which the clear partition was slowly raised. Trials lasted for one hour and were videotaped so there was no human disturbance in the room during the trial. The first 15 minutes of each trial was discarded to allow lizards time to adjust after the partition was raised. For the remaining 45 minutes the amount of time females spent in the left and right side of the middle partition was recorded. Trials were discarded if a female did not visit each male at least once. Two trials were discarded leaving ten trials for analysis.

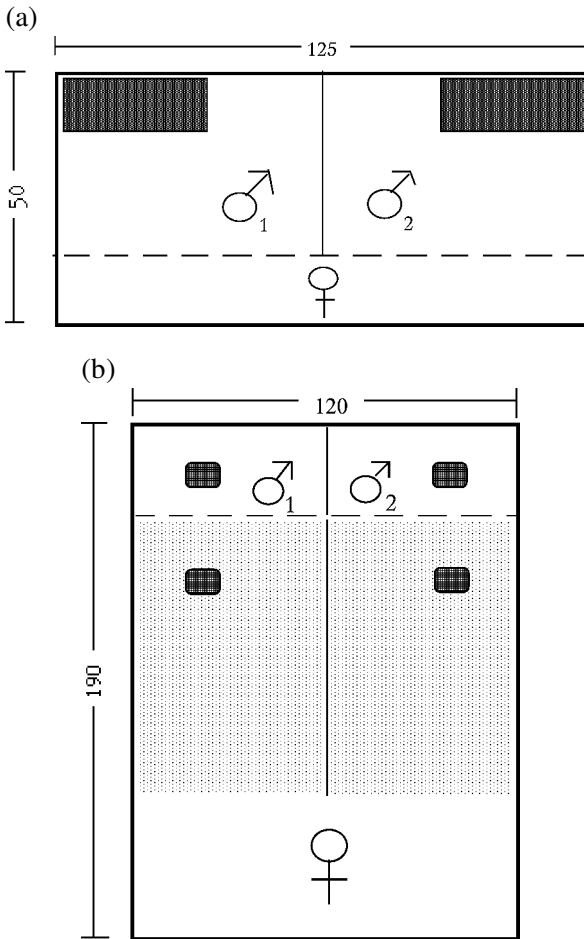


Fig. 1. Test arenas for female mate choice trials, viewed from above. All distances are in cm. (a) Test arena for experiment one. Dark lines indicate solid walls and the dotted line indicates a clear partition which was raised at the beginning of the trials. The dark rectangles indicate bricks for the lizards to sit on. (b) Test arena for experiment two. Dark lines indicate solid walls and the dotted line a clear 'beauty glass' which separated the males and female throughout the trials. Dark rectangles are tiles which lizards could sit on or hide underneath. Shaded areas in front of the male compartments indicate the regions in which a female was considered to have made a choice of the corresponding male.

Experiment 2: Male chest patch area

Lizards were collected in late spring 1998 after lizards had emerged from winter inactivity but prior to oviposition. All females collected had developing follicles. Lizards were housed in a controlled temperature room; males in individual cages and females in groups of eight.

Prior to the mate choice trials lizards were maintained at 20/13°C day/night to slow down moulting and female egg development before the trials commenced. Prior to and following the mate choice trials photoperiod, temperature, heat lamps and diet were the same as for experiment one. Sixteen male lizards collected for the previous mate choice experiment were also used in this experiment.

Mate choice trials were conducted to determine whether the large amount of condition-dependent variation in male chest patch size (see below) was subject to female mate choice. Trials were conducted 31 days after lizards were collected; 25 days after reflectance spectrophotometry and within 24 hours of chest patch size measurement. Males were paired with respect to chest patch size. Each male was used only once and a different female was used for each trial. Of the 20 trials conducted 12 were pairs of males collected in 1998 and 8 were pairs of males collected in 1997. There was no difference in the amount of time females spent with the males collected in 1997 (66.5 ± 3.09 frames) and those collected in 1998 (71.5 ± 3.64 frames; unpaired t test: $t_{18} = -1.04$, $p = 0.31$). Thus in all analyses these trials were pooled. The mate choice trial arena is illustrated in Fig. 1b. The arena consisted of a separate compartment for each male (no visual or olfactory contact) and an area in front of the males in which the female could move freely. A partition partially divided the female's compartment. A line of tape 1.2 m from the edge of the males cages and in line with the end of the partition indicated the area in which a female was considered to have made a choice of that male. This choice zone was determined so that in choosing the area in front of one male the female could not simultaneously view the other male. All lizards had identical tiles to rest on and hide under. These tiles were positioned so that there was no difference between each male's tile position in relation to the female and so that the female had tiles placed identically in front of each male. Chambers were scrubbed with detergent between trials to remove any chemical or faecal secretions.

Chambers were illuminated with True-Lites (Duro-test) which provide full spectrum lighting which is closely matched to sunlight. Males were separated from females by acrylic beauty glass (Hsinhwa) which has a 100% wavelength cut-off at 300 nm and a 50% cut-off at 340 nm; this transmission pattern mirrors that of the cornea and lens of *C. ornatus* (LeBas & Marshall, 2000). The day temperature of the room was 28°C. Further lamps for heating were not provided as this trial involved the choice of a colour trait and no full spectrum heat lamps were obtainable. This is not ideal as lizards would not have been able to thermoregulate to their preferred body temperature (36.6°C, Bradshaw & Main, 1968). However, lizards showed normal activity at this temperature and there were criteria which excluded trials in which females were not associating with males (see below). Furthermore, these trials were testing female preferences for residing within a male's territory and such decisions must be made whenever active; hence preference should be shown over a broad range of temperatures. As females associated with males more than random (see results) this temperature was likely to be adequate for spatial preference to be expressed.

Lizards were allowed to acclimatise to the cages overnight and for one hour the following day. Female position was recorded over two days using a time lapse video camera which recorded images directly to a computer. A frame was taken every 20 min resulting in 40 frames a day for a total of 80 frames per trial. This method minimised disturbance to the lizards as the images were downloaded after the lights had gone off at the end of the first day and this was the only time a researcher was present during the trial period. For each frame females were scored as present in either the left or right male section or the middle neutral section. According to predetermined criteria, trials were discarded if a female lizard was not

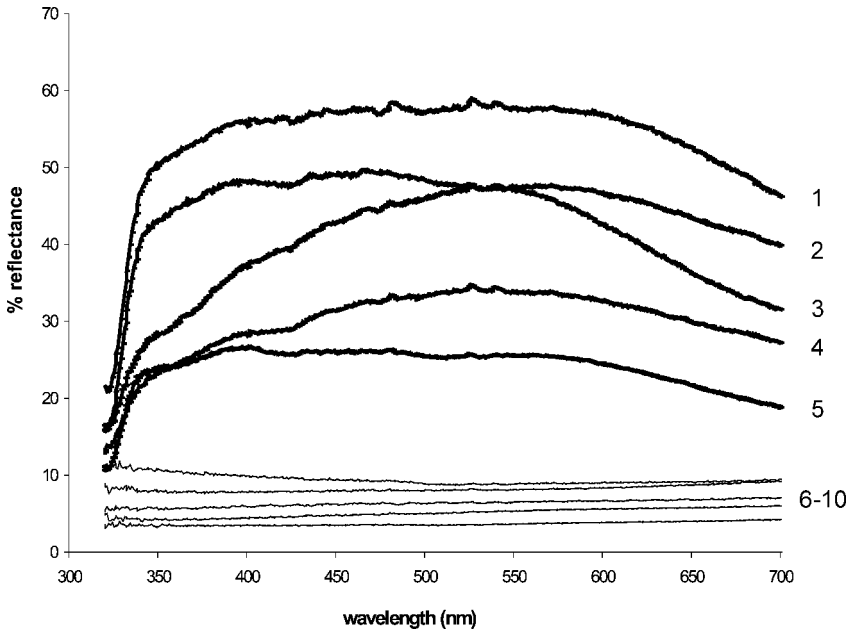


Fig. 2. Variation in reflectance spectra between individual males in the throat (dark lines; curves 1-5) and chest (light lines; curves 6-10). Each curve is an average of three or five reflectance spectra from one male. Standard error bars were removed for clarity. Reflectance curves were chosen to represent the maximum amount of variation in spectral shape between males for each region.

scored at least once in each male's section or if they spent greater than 50% of their time (>40 frames) in the neutral section. Twenty trials were conducted of which two were discarded.

Throat and chest reflectance data were available for ten of the pairs used in the chest patch trials. Three aspects of male colour traits were examined: chest brightness; throat brightness and throat spectral shape. Throat spectral shape was examined due to the high variability in this trait (Fig. 2). Ventral colour traits were examined as these are empathised during displays whereas dorsal coloration appears more likely to be involved in camouflage (LeBas & Marshall, 2000).

All variables were checked for normality. Non-parametric tests were used for variables with non-normal distributions. All tests were two-tailed.

Results

Male traits

Coefficients of variation revealed high variation in chest patch area and low variation in jaw length and head width (Table 1). Male chest and

TABLE 1. Mean \pm standard error (SE) and coefficients of variation (CV) for male traits in *C. ornatus*

Male trait	<i>N</i>	Mean \pm SE	CV
Snout vent length	41	91.3 \pm 0.51	3.61
Weight	41	24.9 \pm 0.45	11.70
Jaw length	41	20.5 \pm 0.14	4.25
Head width	41	18.69 \pm 0.1	3.59
Chest patch – area	40	2.78 \pm 0.11	25.06
Chest patch – brightness	22	3032 \pm 258	39.92
Throat – brightness	23	15961 \pm 879	27.00
Dorsal (white stripe) – brightness	9	11234 \pm 839	22.39
Dorsal (black areas) – brightness	10	1869 \pm 173	29.39

N is number of males measured. Units are mm for morphological traits; grams for weight and cm² for the chest patch area. Brightness measures are dimensionless.

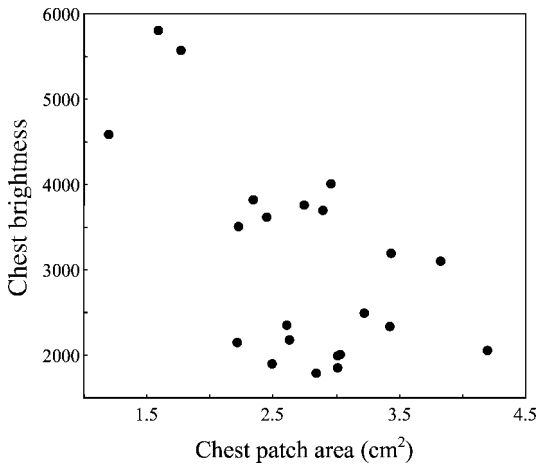


Fig. 3. Spearman rank correlation between chest patch size and chest patch brightness.

throat brightness had high coefficients of variation as did dorsal measures of brightness (Table 1), thus high coefficients of variation may be standard for brightness measures of colour. Visual inspection of the throat and chest reflectance curves showed large variation in spectral shape in the throat but little in the chest (the most variable curves in regard to spectral shape are graphed in Fig. 2).

Males with larger chest patches had chests which were less bright i.e. were a darker black (Fig. 3; Spearman rank correlation: $Rho = -0.47$, $N = 22$,

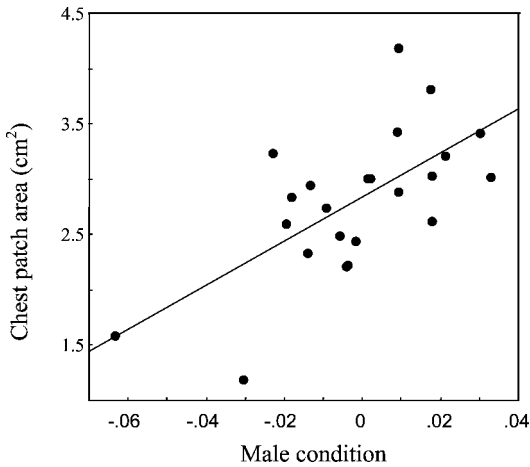


Fig. 4. Least squares regression of male chest patch size on male condition. This relationship is maintained with a Spearman rank correlation which is not influenced by outlying data points.

$z = -2.14$, $p = 0.03$). There was no relationship between the chest patch size and SVL (Pearson's correlation: $r = 0.12$, $N = 24$, $p = 0.57$).

Males that were in better condition had larger chest patches (Fig. 4; Least squares regression: $F_{1,22} = 15.63$, $r^2 = 0.43$, $p = 0.0007$). There was no relationship between, condition and chest patch brightness (Spearman rank correlation: $Rho = -0.36$, $N = 21$, $z = -1.58$, $p = 0.11$). Neither was there a relationship between condition and throat brightness (Least squares regression: $F_{1,21} = 1.40$, $r^2 = 0.07$, $p = 0.25$) or spectral shape (Least squares regression: $F_{1,21} = 0.26$, $r^2 = 0.01$, $p = 0.61$). Thus chest patch size is the only trait that reliably signals male condition. This result is maintained after sequential Bonferroni adjustment for the number of tests (Rice, 1989).

Experiment 1: Male size

There was no difference in the time females spent with large (20.1 ± 5.36 min) and small males (24.9 ± 5.36 min; Paired t test: $t_9 = -0.445$, $p = 0.66$, Fig. 5).

Experiment 2: Male chest patch

Females spent significantly more time (number of frames) in the sections closest to the males than in the neutral section (one group t test on arcsin

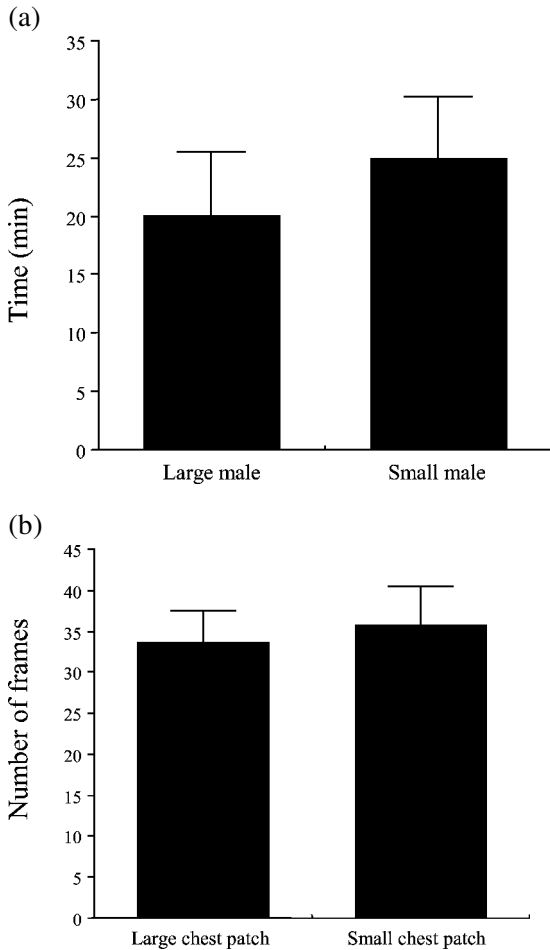


Fig. 5. (a) The mean number of frames (\pm SE) that a female spent with the large and small SVL male. (b) The mean amount of time (\pm SE) that a female spent with the large and small chest patch male.

transformed data with expected value arcsin (66.66%): $t_{19} = 5.55$, $p = 0.001$). This finding indicates that females were interested in the males rather than aimlessly wandering about the enclosure.

There was no difference in the time females spent with males with large (33.7 ± 3.78 frames) and small chest patches (35.83 ± 4.71 frames; Paired t test: $t_{17} = -0.26$, $p = 0.8$; Fig. 5). The test had sufficient power (0.82) to detect a difference of the same magnitude as what we found for male

choice of females in the same experimental design (LeBas & Marshall, 2000) (power calculated according to Zar (1984)).

There was no difference in the time females spent with males with bright (29.7 ± 5.84 frames) and dull chest patches (38 ± 5.51 frames; Paired t test: $t_8 = -0.746$, $p = 0.48$). For the throat there was no difference in the time females spent with bright (37.4 ± 7.04 frames) or dull males (31.6 ± 5.87 frames; Paired t test: $t_9 = 0.454$, $p = 0.66$). However, in eight of ten trials females associated with the male with the highest PC2 score for the throat. Males with a higher PC2 score had reflectance curves which peaked in the short (blue) rather than the long (red) wavelengths (curves 2 and 5 in Fig. 2). Females spent a greater number of frames with males with a high PC2 score (46.3 ± 4.93 frames) than with males with a low score (22 ± 3.86 frames; Paired t test: $t_9 = 2.80$, $p = 0.02$), though this difference is not significant after sequential Bonferroni adjustment for the number of tests on this trial (Rice, 1989).

Discussion

In *C. ornatus* chest patch size is highly variable amongst males and reliably indicates male condition. Male's with a larger chest patch also had a patch which was a darker black. In the lizard *Psammodromus algirus*, male's which were given a testosterone implant had larger colour patches than controls (Salvador *et al.*, 1996). However, it has also been shown in lizards that males with experimentally increased testosterone levels lose more weight, have lower survival and gain more parasites than control males (Marler & Moore, 1988; Salvador *et al.*, 1996). If chest patch size and darkness are dependent on testosterone levels in *C. ornatus*, it may be that males in better condition can carry the costs of high testosterone levels and hence express the bigger trait.

Traits which reliably signal male condition have been found in numerous taxa often along with female preference for the trait (Andersson, 1994; Mappes *et al.*, 1996; David *et al.*, 1998). We found no evidence in *C. ornatus* for female choice of males on the basis of their condition-dependent chest patch size. As far as we are aware the only other condition-dependent trait which has been found in lizards is in the sand lizard where the area of green on a male's side (referred to as a 'badge') was positively correlated with

male condition (Olsson, 1994). In sand lizards the badge indicated males with higher fighting ability (Olsson, 1994). Similarly, male tree lizards with a larger blue spot on their dewlap won more male contests (Thompson & Moore, 1991). In *C. ornatus* the chest patch is clearly exposed by the push-up displays males continuously perform to one another during conflicts (LeBas, unpubl. data). Field studies reveal males with a larger chest patch have larger territories and more females within the territory (LeBas, 2001). It is hence likely that in *C. ornatus* also, chest patch size is used by males to assess one another's condition and thus perhaps fighting ability. The higher number of females within a male's territory is also likely to reflect the male's ability to defend these females rather than female choice for these males.

We can envisage two reasons why female *C. ornatus* may not associate with males with respect to their chest patch size. First, if male chest patch size is important in male contests it may be that females are primarily choosing territory size or quality and hence mating with better condition males (with large chest patches) without direct choice of the condition-dependent trait. Second, females may refine their choice amongst the territory holders by choosing on other traits. However, we found no evidence for female choice of a range of male traits including: male size; throat or chest brightness or throat hue. Nevertheless, there was a trend for females to associate with males with 'bluer' throats. Unfortunately we were unable to test female choice of males immediately following reflectance spectrophotometry of this trait. Hence, given the time period between measurement and testing, we cannot attach more surety to this result other than to suggest it warrants further investigation. Traits which were tested for female choice were those considered most likely to be subject to sexual selection. Chemical cues have been recently found to be involved in mate choice in lizards (Martín & Lopez, 2000) and may also warrant further investigation.

In the field, larger males had higher reproductive success, despite not having larger territories or more females in their territory (LeBas, 2001). This higher reproductive success was instead the consequence of a greater number of extra-territorial matings (LeBas, 2001). Furthermore, when females sired offspring with an extra-territorial male, this male was significantly larger than the female's territorial partner (LeBas, 2001). The finding of the study presented here suggests the higher reproductive success of larger males is not a consequence of female choice. Rather, it may be that larger males in the field have higher success at breaching other males territories and gaining

access to females (LeBas, 2001). Alternatively, female preference for larger males may not be expressed when given the choice to spatially associate with males.

The lack of finding for female preference of male traits in this study may be due to the context in which choice was examined. As discussed in the methods spatial association is likely to be a meaningful reflection of female preference of mate in this species, however random spatial association with males and instead choice of partner during a short receptive period cannot be excluded. Female spatial association with males is indicative of a female choosing her territorial partner. As this study has shown no such associations with respect to a range of male traits, further study of female choice in this species should investigate female choice quantified as copulations or offspring sired, whilst controlling for male territory variables. At this stage it can be concluded that female's do not spatially associate with males with regard to the male traits upon which female choice would be most expected.

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