

Ecological divergence among colour morphs mediated by changes in spatial network structure associated with disturbance

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Summary

1. Differences in individual behaviour affect social interactions and contribute to the spatial structuring of animal populations. However, disturbance should also affect spatial networks by altering habitat heterogeneity and resource availability. Variation in resource availability should perturb the frequency and nature of social and ecological interactions within a population by affecting the spatial distribution of individuals.

2. In disturbed habitats where resources are limiting, spatial relationships should reflect behavioural differences among individuals, with higher-quality resources controlled by dominant individuals. In contrast, all individuals may exploit preferred resources in resource-rich habitats. Environmental variation and population reorganization may also result in variation in morphological, behavioural and ecological traits, which ultimately affect fitness.

3. We addressed these considerations for male tree lizards (*Urosaurus ornatus*) at three sites that differ in levels of disturbance. The habitats at these localities differed in the availability of live trees, the preferred microhabitat of *U. ornatus*. In addition, male *U. ornatus* exhibits a polymorphism in dewlap colour linked with differences in aggression, which should influence their position in a network and access to resources. We applied a network framework to characterize the spatial organization of male morphs at each site and quantified male aggressive behaviour in the laboratory. We also compared body size, body condition, number of bite marks, parasite load and the microhabitat use and diet, of males among the sites.

4. We detected no significant differences in spatial network structure between unburned and infrequently burned sites. However, at a frequently burned site, the network shifted towards geographically closer, heteromorphic male neighbour associations. Males at this site were also larger, more aggressive and had more bite marks but fewer parasites than males at the other sites. Moreover, we detected divergence in microhabitat use and diet among the morphs at the frequently burned site that reflected the shift in spatial network structure and differences in morph behaviour. That is, only more aggressive morphs usurped trees and consumed prey from higher trophic levels.

5. We conclude that environmental variation may influence animal spatial network structure. Jointly, behavioural and environmental variation may promote despotic social dynamics and ecological divergence in resource-limited habitats.

Key-words: behaviour, colour polymorphism, diet, prescribed fire, stable isotope analysis, *Urosaurus ornatus*

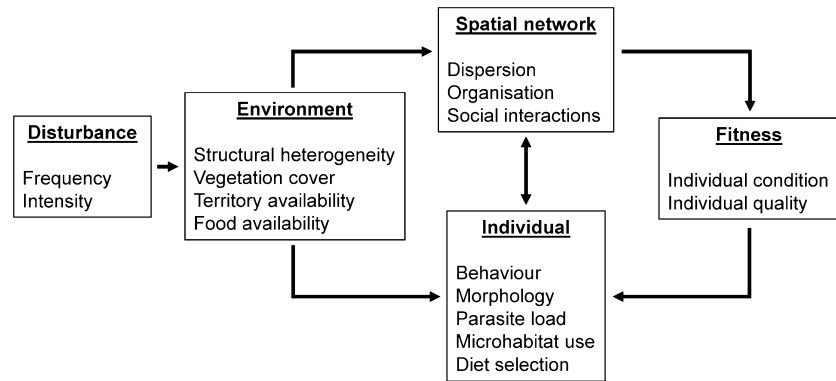
Introduction

A growing number of studies have demonstrated that non-random differences in individual behaviour affect population structure (reviewed in Krause, James & Croft

2010). Across several taxa, individual differences in aggressive behaviour appear to modulate the social and spatial organization of populations (Pike *et al.* 2008; Croft *et al.* 2009). Moreover, variation in population organization may affect individual fitness, including risk of parasitic infection (e.g. Fenner, Godfrey & Bull 2011). Although these studies provide insight into factors

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Fig. 1. Relationships between the environment, individual organisms, spatial network structure and fitness. Disturbance may influence network structure and individual traits through effects on the structural heterogeneity and resource availability of the environment.



structuring animal populations, the role of environmental variation in population structuring has received scant attention outside of a laboratory setting (Edenbrow *et al.* 2011; Webster *et al.* 2013). Few studies have evaluated how environmental variation resulting from disturbance interacts with individual-level traits to influence spatial population structure.

Disturbance affects habitat heterogeneity and resource availability, which should influence individual behaviour as well as the spatial relationships among individual organisms (Fig. 1; Godfrey, Sih & Bull 2013). Changes in behaviour and spatial relationships should then perturb the nature and frequency of social interactions within the population. For example, habitat openness is associated with greater frequencies of display behaviour and rates of male–male competition in guppies (*Poecilia reticulata*, Edenbrow *et al.* 2011). In another study, Webster *et al.* (2013) demonstrate that more structured habitats cause patterns of information transmission within stickleback (*Gasterosteus aculeatus*) shoals to match their social structure. A consequence of variation in spatial proximity within a network is a change in an individual phenotype and ultimately fitness, such as individual quality (through parasite transmission, Fenner, Godfrey & Bull 2011) and condition (through injuries due to combat, Cañon Jones *et al.* 2010) (Fig. 1). In addition, variation in resource availability and spatial population structure should also affect an individual's access to preferred prey and microhabitat resources. If disturbance leads to resource limitation, then the spatial distribution of individuals relative to these resources should reflect their behavioural differences. Consequently, individuals differing in behaviour will differ in microhabitat use and diet, with higher-quality habitats and/or prey items usurped by dominant individuals. In this scenario, individuals are no longer capable of exploiting any resource due to competitive differences, and thus, the socio-spatial structure of the population reflects a despotic distribution (Fretwell 1972).

The socio-spatial dynamics of territorial species reflect an interaction between individual behaviour and resource availability and should be sensitive to the effects of disturbance. Territory defence is costly (Fretwell 1972), and only dominant individuals consistently monopolize access

to high-quality resources (Calsbeek & Sinervo 2002a). However, because individuals that are more similar to each other are more likely to compete over the same resources (e.g. Schluter 1994), they may suffer a higher cost of interaction relative to dissimilar individuals (e.g. Smith & Parker 1976). For example, Fenner, Godfrey & Bull (2011) demonstrated parasite transmission was limited to within-phenotype subgroups: dispersers were more likely to transmit nematodes to other dispersers, and residents were more likely to transmit mites to other residents. Costs may be enhanced for more aggressive phenotypes that escalate social interactions (Lailvaux *et al.* 2004). Aggressive phenotypes should therefore interact less often with each other in a population (e.g. Godfrey *et al.* 2012; see also Pike *et al.* 2008; Croft *et al.* 2009 for example bold vs. shy individuals). Individuals differing in aggressiveness should therefore differ in their relative position in a network as well as their ability to exploit preferred microhabitat or food resources.

Several lizard species exhibit a polymorphism where males that differ in dewlap colour exhibit discrete behavioural phenotypes associated with alternative mating strategies (Thompson & Moore 1991; Sinervo & Lively 1996; Miles *et al.* 2007). In the tree lizard, *Urosaurus ornatus*, male dewlap colour is genetically based and fixed at maturity (Thompson, Moore & Moore 1993) and reflects differences in aggression: blue males are aggressive and territorial, orange males are nomadic and yellow morphs occupy the interstices of blue male territories (Moore, Hews & Knapp 1998). Blue males use display behaviour, for example head-bobs and fullshows, to establish dominance and defend territories. However, contests between males often escalates to chasing and biting (Thompson & Moore 1991). Orange males are nomadic and may establish home ranges throughout the habitat; however, they may switch to territorial defence when habitat resources are abundant (Moore, Hews & Knapp 1998). Fewer observations are available regarding the behaviour of yellow males other than their satellite tactic. Observations of yellow morph males at our study site suggest that they are capable of usurping the territory of a blue male, based on their aggressive behaviour towards blue males during staged resource contests in the laboratory (M. S.

Lattanzio & D. B. Miles, unpublished data). This strategy may be in response to blue male display behaviour (Smith & Parker 1976), which could be advantageous and allow a yellow male to usurp the microhabitat or prey resources within a blue male's territory.

We investigated the consequences of disturbance (historical burn frequency) on the spatial, social and ecological dynamics outlined in Fig. 1 for the three male *U. ornatus* colour morphs. We used capture data to describe the structure of male *U. ornatus* spatial networks at three sites differing in prescribed fire history. We evaluated whether resource-limited burned sites are associated with the spatial reorganization of morphs within a population towards a despotic distribution. We also tested for differences in male traits associated with competitive ability (body size and aggression) among the sites to explore whether resource limitation is associated with increased resource competition. Next, we explored the fitness consequences of variation in network structure by testing for differences in body condition [residuals from the regression of mass against snout-vent length (SVL)], number of bite marks (evidence of territorial disputes) and ectoparasite load (a measure of stress and ability to mount an immune response) of male lizards among the sites. Finally, because shifts in network structure associated with environmental variation may feedback into ecology (e.g. Fig. 1), we tested for morph differences in two ecological traits linked with territory and home range quality: microhabitat use and diet selection. Our estimates of microhabitat use involved in determining the proportion of males that occupied live (preferred) or dead (snag) trees. We used stable isotope analysis to quantify diet differences among the colour morphs at each site. Our results provide insight into how behavioural and environmental variation may shape animal spatial networks in the wild and that jointly these factors may favour despotic social dynamics leading to ecological divergence in resource-limited habitats.

Materials and methods

HABITAT DESCRIPTION

We surveyed three sites that differ in vegetation cover as a consequence of differences in prescribed fire history (Table S1, Supporting information) at the Appleton-Whittell Research Ranch in Santa Cruz County, Arizona. These sites include the following: a non-burned site (since 1970, hereafter NB), a site burned once in 2002 [Low-frequency burn (LB)] and a site burned in 1997 and again in 2002 [High-frequency burn (HB)]. The same burn affected both LB and HB sites in 2002. The study localities differ in environmental heterogeneity as a consequence of burn regime (principle response curve analysis comparing vegetation and structural cover among the sites from 2010 to 2012, $F_{6,279} = 17.66$, $P < 0.001$). Although live trees (*Quercus* and *Prosopis* spp.) are common at the NB site, a history of prescribed fire has favoured the domination of grasses over other vegetation types at the LB and HB sites (>70% grass cover, Table S1,

Supporting information). Environmental heterogeneity (including live tree cover) is lowest at the HB site. All sites are similar in elevation and share similar soil and topographic characteristics.

LIZARD CAPTURE

We captured adult male *U. ornatus* from the three study sites between June and July 2012. We sampled during this time of year to ensure all territories and spacing patterns of males had stabilized. Each site is separated by at least 3 km, which exceeds the known dispersal distances for *U. ornatus* (Zucker 1989). We also surveyed the periphery around each site (c. 50 m distance away from site edge) to ensure we captured all individuals and detect potential dispersal away from the sites. We noose- or hand-captured all lizards and georeferenced all capture points using a hand-held GPS unit (Garmin GPSMAP 60CSx; Garmin Ltd., Chicago, IL, USA). We housed individual lizards overnight in a laboratory facility in separate 5.7 L aquaria (27.9 cm L × 17.8 cm W × 12.7 cm H; Frey Scientific, Nashua, NH, USA). Lizards were provided water *ad libitum*. We released all animals at the site of capture.

SPATIAL NETWORKS

Male *U. ornatus* defend small territories or home ranges around a central tree (live or dead) (c. 5–10 m between neighbouring territories, M'Closkey, Baia & Russell 1987), and mark-recapture data indicate that initial capture points are representative of male territory spacing patterns throughout the breeding season (Table S2, Supporting information). Moreover, frequent social interactions are common between neighbouring males (Zucker 1989; M. S. Lattanzio, personal observation), and the geographic proximity among males reflects the degree of social interaction between them in a population. We used the latitude and longitude coordinates of each lizard's initial capture point to estimate the structure of the *U. ornatus* spatial network at each site (Pike *et al.* 2008; Fenner, Godfrey & Bull 2011). Connections (edges) in our networks represent geographic distances (measured to nearest 0.1 m) between all lizards captured at each site (nodes, $n \geq 28$ per site). Geographic distances were calculated from the latitude and longitude data using the program GEOGRAPHIC DISTANCE MATRIX GENERATOR version 1.2.3 (Ersts 2013). Edge weights were assigned to connections between lizards (nodes) by modifying the protocol of Fenner, Godfrey & Bull (2011) to fit the territory size of our study species (c. 10 m diameter) and to account for precision error on our GPS instrument (Fenner, Godfrey & Bull 2011) (Table 1). We utilized a maximum distance cut-off of 50 m for edge weight assignment because males >50 m apart do not interact (M'Closkey, Baia & Russell 1987; M. S. Lattanzio,

Table 1. Rankings of edge weights, based on geographic distances, used to construct spatial networks of male *Urosaurus ornatus* lizards

Distance (m)	Edge weight
>50	0
40–50	1
30–40	2
20–30	3
10–20	4
0–10	5

unpublished data). This protocol ensured that greater weight was placed on lizards in closer geographic proximity to one another that should interact more often (Fenner, Godfrey & Bull 2011). We specified undirected networks because nearby males may be equally likely to initiate a social interaction (Godfrey *et al.* 2012), as is known in *U. ornatus* (Hover 1985).

We retained four measures of association to describe individual connectedness in the network at each site: degree and eigenvector centrality, strength and mean strength. Degree centrality refers to the number of edges connected to each lizard (Wey *et al.* 2008). Eigenvector centrality provides an index of how connected each individual is to the entire network (Bonacich 1972). Individuals that are more connected (more edges between them and other individuals which also have more edges) will have larger values. Although strength usually refers to the number (or presence) of interactions between pairs of individuals in a network, strength may also be estimated using geographic proximity between individuals (e.g. Pike *et al.* 2008; Fenner, Godfrey & Bull 2011). We calculated individual strength by summing all edge weights that connect to each individual (i.e. node) (Fenner, Godfrey & Bull 2011). We also retained the average weight (mean strength) of all edges connected to each individual. Strength provides an estimate of how connected each male is to other lizards in the network, and mean strength provides an estimate of the average magnitude of those associations (Pike *et al.* 2008; Fenner, Godfrey & Bull 2011). Thus, a large value for strength could indicate either several males that are geographically distant from each other that may rarely interact, or a few males with overlapping territories that should interact often. Individuals with higher mean strength have closer neighbours within a network.

MORPHOLOGY

We recorded body size (SVL) to the nearest 0.1 mm using callipers and mass to the nearest 0.1 g using a Pesola™ scale (Pesola AG, Baar, Switzerland) of each lizard we captured.

DOMINANCE BEHAVIOUR

We size-matched pairs of males ($\Delta_{\text{SVL}} \leq 2.0$ mm) and subjected them to contests for access to a limited resource (following Robson & Miles 2000). We assigned males to one of three morph dyads for each trial at random: B-B, B-O or B-Y. We did not include an O-Y dyad because dominance interactions and territorial disputes in this species typically involve a B male and another male morph (B, Y or O) (Thompson & Moore 1991; Thompson, Moore & Moore 1993). We staged contests using a small, circular plastic tank (0.2 × 1.2 m, depth × diameter), with sand as a substrate and a central perch (raised branch), with a heat source (100 W light) suspended *c.* 0.4 m above the perch. The lamp generated a thermal gradient in the arena ranging from 22 °C at the periphery to 42 °C on and under the perch. This gradient encouraged the lizards to move towards the central perch, encounter one another and initiate competition for the perch (Robson & Miles 2000). We placed each male at opposite ends of the arena and covered them with opaque plastic cups. A trial was initiated by simultaneously lifting these containers. We recorded the behaviour of each male beginning at this point and for a total of 30 min from behind a blind. Because we size-matched males, our experimental design necessitated that some males be used in more than one trial, but no males were used more than twice.

We recorded the number of times each lizard used the following aggressive behaviours: display – head-bob, lateral (raised posture with lateral flattening of body sides) and fullshow (push-ups in a laterally flattened posture to expose ventral colour patches) and escalation – chase and bite. These behaviours are described in detail elsewhere (Carpenter & Grubitz 1961; Martins 1993). We considered the lizard that occupied the perch at the end of the trial as the winner.

MALE CONDITION AND QUALITY

We retained the residuals of the regression of log mass with log SVL as our estimate of body condition. Dominance interactions and territorial contests between blue morph male *U. ornatus* territory holders and other male morphs are common in the wild (Zucker 1989; Thompson & Moore 1991), and these interactions often escalate to biting (Deslippe *et al.* 1990; Lattanzio, personal observation). Bite marks from *U. ornatus* lizards are small and exhibit a characteristic V-shape that is distinct from bites by other species, including predation attempts (e.g. Fig. S1, Supporting information). We counted the number of bite marks on each lizard that could be attributed to other *U. ornatus* as an estimate of the magnitude of interactions among males at each site. Male *U. ornatus* lizards also vary in intensity of infection by ectoparasitic mites. Ectoparasite load may be influenced by both individual behaviour and environmental conditions (Fenner, Godfrey & Bull 2011; Garrido & Pérez-Mellado 2013). The patterns of ectoparasite infection may differ among the morphs, study sites or both. For each lizard, ectoparasite load was quantified as (i) the total number of distinct body regions (e.g. limb joints, skin folds) where mites were identified and (ii) the rank abundance of mites across all of these body regions. Rank abundance was scaled 0–6 (rank in parenthesis): no mites (0), 1–5 mites (1), 6–10 mites (2), 11–15 mites (3), 16–20 mites (4), 21–25 mites (5) and >25 mites (6).

MICROHABITAT USE AND DIET SELECTION

Because male *U. ornatus* prefer to establish home ranges in trees (M. S. Lattanzio & D. B. Miles, unpublished data; Herrel, Meyers & Vanhooydonck 2001), variation in the availability of trees is an indication of habitat quality. At our study sites, *U. ornatus* use either live trees or snags (fallen trees). We also assume that lizards captured on live trees occupy higher-quality microhabitats than lizards captured on snags. We recorded the microhabitat use (tree or snag) of each lizard upon capture.

We toe-clipped all males used in this study for unique identification prior to release. We followed current guidelines for the care and use of animals for toe-clipping, and there is no evidence that toe-clipping affects performance or survivorship in lizards (Massot *et al.* 1992). Estimates of diet selection were obtained by analysing the claws from these toe clips for their carbon and nitrogen stable isotope composition. Claws were oven-dried at 60 °C until they reached a constant mass (*c.* 48 h), weighed and then transferred into separate 5 × 8 mm tin capsules (Costech Inc., Valencia, CA, USA). These samples were analysed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values using a PDZ Europa ANCA-GSL elemental analyser interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd., Crewe, Cheshire, UK) at the University of California Davis Stable Isotope Facility (<http://stable-isotopefacility.ucdavis.edu>). The error deviation for $\delta^{13}\text{C}$ was

0.2‰ and 0.3‰ for $\delta^{15}\text{N}$. All isotopic values generated by this analysis are expressed in standard per mil delta (δ) notation,

$$X_{\text{‰}} = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000_{\text{‰}}$$

where $X = \delta^{13}\text{C}$ or $\delta^{15}\text{N}$, and $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{15}\text{N}/{}^{14}\text{N}$, respectively.

STATISTICAL ANALYSIS

We compared the frequency of B, O and Y male morphs among the three sites with a multinomial test.

We analysed variation in connectivity (degree and eigenvector centrality) of the network at each site using a nonparametric multivariate analysis of variance (function ‘adonis’ in the *VEGAN* package, Oksanen *et al.* 2012) with site and morph as factors. For this analysis, we generated a distance matrix from connectivity data using the Bray–Curtis coefficient because it is robust to differences in patterns of variance in the data (Bray & Curtis 1957). Here, higher values for this coefficient reflect greater percentage of similarity among pairs of individual lizards in how connected they were in each network at each site. For this analysis, we specified 4000 permutations and limited randomization to within-sites. The strength (number of edges connecting to a node) and mean strength (average number of all edges directly or indirectly connected to a node) of each network were analysed using separate permutation *F*-tests. These tests evaluated the prediction that territorial B males differed in their patterns of integration within the spatial network at each site. One pattern is that B males cluster with one another, whereas another is that B males associate more often with either O or Y males. We included neighbour identity (i.e. B, O or Y morph) as a factor in addition to site in our analyses of strength and mean strength.

Separate ANOVAs were used to compare variation in male body size (log-transformed SVL) and body condition, with morph and site as factors. A MANOVA was used to compare the frequencies of aggressive behaviours (head-bob, lateral, fullshow, chase and bite behaviours) during social contests, with site (HB, LB or NB), status (winner or loser) and male dyad (B-B, B-O or B-Y) as factors. We also included individual identity as a categorical predictor in this analysis to account for repeated use of some males in these social contests.

The number of injuries (bite marks, count data) were analysed using a Poisson regression with morph and site as factors. We compared our estimates of ectoparasite load (number of infected body regions and rank-total mite number) using separate regressions with site and morph as factors. For rank-total mite number, we specified an ordinal regression (function ‘lrm’ in the *R* package *RMS*, Harrell 2014) and for number of infected body regions we used a quasi-Poisson regression. We did not use an ordinal regression in the latter case because number of body regions refers to the raw, not ranked, counts of body regions with mites.

Differences in microhabitat use (tree or snag) were evaluated using chi-square statistics across the sites by each morph. We used an ANOVA to test whether lizards using trees vs. snags differ in body size. We included a perch type \times site interaction term in this model to account for site-specific differences in the relationship between SVL and perch use. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of consumer tissues used to reconstruct diet are influenced by variation in the isotopic composition of base resources (Post 2002). We compared *U. ornatus* diets at different sites by calculating the trophic

position of each lizard relative to the isotopic values of vegetation collected from the same site as the lizard (Post 2002). The vegetation at the study site consists of C_3 (tree, shrub and forb) or C_4 (grass) photosynthetic pathways. The proportions of these vegetation types, and their isotopic signals, differed among the study sites (Table S1, Supporting information). The trophic position of a lizard may be estimated from the mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from C_3 and C_4 vegetation at each site using formula (eqn 1):

$$\lambda + (\delta^{15}\text{N}_{\text{lizard}} - [\delta^{15}\text{N}_{\text{C}_4} \times \alpha + \delta^{15}\text{N}_{\text{C}_3} \times (1 - \alpha)]) / \Delta^{15}\text{N} \quad \text{eqn 1}$$

where α is the proportion of nitrogen derived from C_4 base resources, λ is the trophic position of the base resources ($\lambda = 1$ for primary producers), and $\Delta^{15}\text{N}$ refers to the expected change between consumer and diet isotope values with each trophic step (discrimination factor, Tieszen *et al.* 1983). We estimated the diet–tissue fractionation ($\Delta^{15}\text{N}$) by *U. ornatus* claw tissues in a separate study ($\Delta^{15}\text{N} = 0.7_{\text{‰}}$; M. S. Lattanzio & D. B. Miles, unpublished data). Carbon isotopes may be used to estimate alpha (α), where $\alpha = (\delta^{13}\text{C}_{\text{lizard}} - \delta^{13}\text{C}_{\text{C}_3}) / (\delta^{13}\text{C}_{\text{C}_4} - \delta^{13}\text{C}_{\text{C}_3})$ (Post 2002). The trophic position for each population was compared using an analysis of covariance (ANCOVA) with morph and perch type (tree or snag) as factors. We included SVL as a covariate in this model because body size may influence diet selection in lizards (Costa *et al.* 2008).

All statistical procedures were conducted in *R* (R Development Core Team 2012). All *post hoc* pairwise comparisons are interpreted using Tukey’s HSD test-adjusted *P*-values (hereafter P_{adj}).

Results

MORPH FREQUENCIES

The frequencies of B, O and Y males did not differ among the study sites (multinomial test, $\chi^2 = 2.79$, d.f. = 4, $P = 0.6$). However, we observed a decrease in B male and increase in Y male frequency between the NB and the HB site (Fig. 2).

SPATIAL NETWORKS

Male spatial networks differed among the sites (Fig. 3; Table S3, Supporting information). These networks had a mean density of 0.21 and thus accounted for 21% of all possible edges at each site.

We detected significant differences in connectivity (degree and eigenvector centrality) among lizards by site (adonis, site: $F_{2,78} = 8.36$, $P = 0.001$; all else $P > 0.18$). No other factors emerged as being statistically significant. Lizards at the NB site have more edges (connections) than lizards at the LB site ($P_{\text{adj}} < 0.001$). Individual lizards within all three sites overlapped in eigenvector centrality ($P_{\text{adj}} > 0.5$), which suggests all morphs exhibited a similar pattern of integration within the network at each site.

We found no difference in strength among B males having B, O or Y neighbours (i.e. pooled across all three study sites, permutation test, $F_{2,67} = 1.83$, $P = 0.112$). However, B males differed in strength among the sites (permutation test, $F_{2,67} = 2.97$, $P = 0.048$; Table S3,

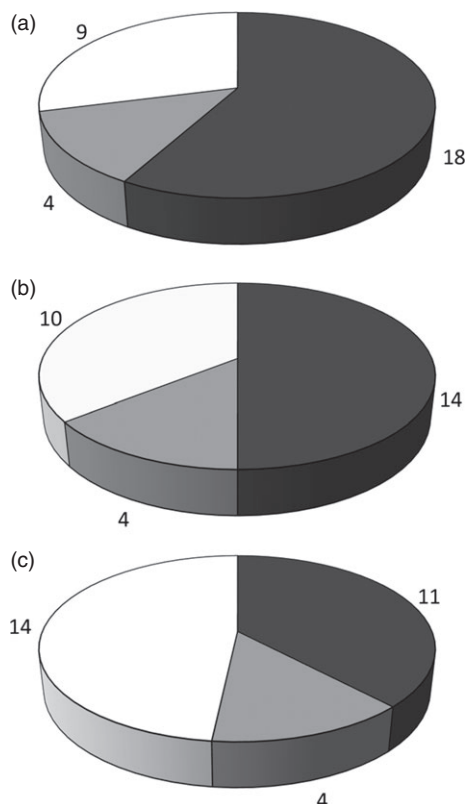


Fig. 2. Frequencies of male *Urosaurus ornatus* at the study sites. Sites include a non-burned control (a), low-frequency burn (b) and high-frequency burn (c) site. Pie slices are shaded by male colour morph: blue (dark grey), orange (light grey) and yellow (white). Numbers outside of slices indicate sample size.

Supporting information), with B males having a higher strength at the HB site relative to the LB site ($P_{\text{adj}} = 0.05$). The analysis revealed an interaction between burn regime and neighbour identity with respect to strength (permutation test, $F_{4,67} = 2.68$, $P = 0.016$). Blue males overlapped more with Y males than B males at the HB site ($P_{\text{adj}} = 0.05$). In addition, B males showed higher overlap with Y males at the HB site than B males had with O males at the NB site ($P_{\text{adj}} = 0.01$).

We detected similar patterns for mean strength across the sites (permutation test, $F_{2,67} = 9.87$, $P < 0.001$; Table S3, Supporting information). Blue males had closer neighbours at the HB site relative to B males at either the LB or NB site ($P_{\text{adj}} < 0.001$ and $P = 0.003$, respectively). We did not detect a difference in mean strength among B males neighbouring B, O or Y males (permutation test, $F_{2,67} = 1.68$, $P = 0.141$), but the interaction between site and morph was significant (permutation test, $F_{4,67} = 3.46$, $P = 0.007$). Blue males had closer neighbours that were Y males at the HB site than B males with B or O neighbours at the LB site ($P_{\text{adj}} = 0.015$ and 0.026 , respectively). In addition, B males had closer neighbours that were O males at the HB site compared to B males with O or B neighbours at the LB site ($P_{\text{adj}} = 0.001$ for both cases), and B males with B or Y neighbours at the NB site ($P_{\text{adj}} = 0.008$ and 0.004 , respectively).

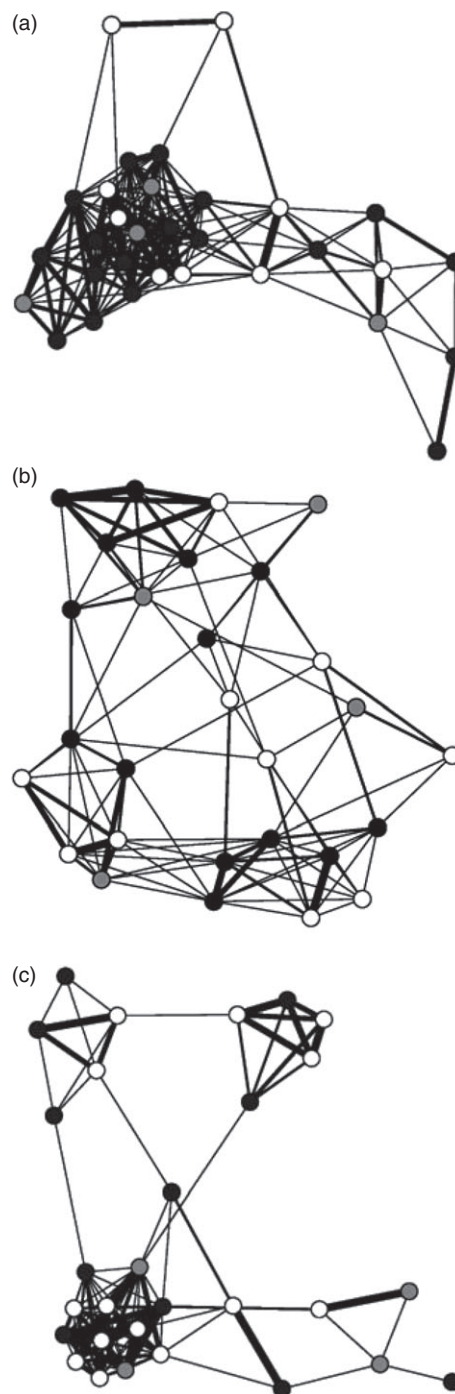


Fig. 3. Male tree lizard (*Urosaurus ornatus*) spatial networks at the study sites. Sites include a non-burned control (a) ($n = 31$), a low-frequency burned (b) ($n = 28$) and a high-frequency burned (c) ($n = 29$) site. Nodes (georeferenced lizard capture points) are shaded by male colour morph: yellow (white nodes), orange (light grey nodes) or blue (dark grey nodes). Edges (connections) are weighted by the geographic distance between lizards (thicker lines indicate closer proximity, following Table 1).

MORPHOLOGY

Body sizes of male lizards differed among the sites but not among morphs (ANOVA, site: $F_{2,79} = 8.93$, $P < 0.001$; morph: $F_{2,79} = 0.214$, $P = 0.808$; site \times morph: $F_{4,79} =$

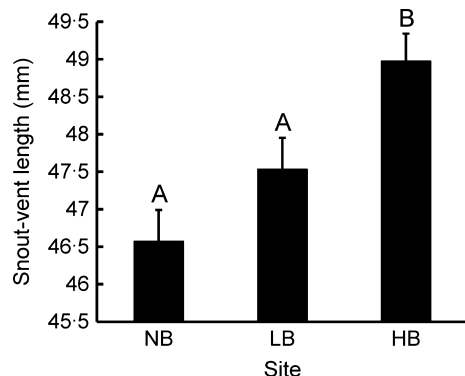


Fig. 4. Body size (snout-vent length, mm) of male *Urosaurus ornatus* lizards captured at the three study sites. Sites include a non-burned control (NB) ($n = 31$), low-frequency burned (LB) ($n = 28$) and high-frequency burned (HB) ($n = 29$) site. Letters above bars denote significant pairwise differences at $\alpha = 0.05$ (see Results). Points are mean ± 1.0 SE.

0.562, $P = 0.691$). Males at the HB site were larger compared with the other two sites (HB vs. LB, $P_{\text{adj}} = 0.049$; HB vs. NB, $P_{\text{adj}} < 0.001$; Fig. 4).

DOMINANCE BEHAVIOUR

Fullshow behaviour was common during dyadic contests (70.4% of all behaviours). In contrast, escalation to biting was infrequent (3.2% of all behaviours). Winners exhibited more display and escalate behaviours than losers (MANOVA, $F_{1,12} = 12.89$, $P = 0.001$; all $P_{\text{adj}} < 0.05$; Fig. 5). Male behavioural patterns during these contests differed by site (MANOVA, $F_{2,12} = 3.1$, $P = 0.018$). Males at the HB site tended to escalate contests by chasing and biting each other more often than males at the NB site ($P_{\text{adj}} = 0.03$ and 0.011 , respectively). Males at the HB site also escalated to biting more often than males at the LB site ($P_{\text{adj}} = 0.008$). We observed no differences in behavioural patterns among the dyads (MANOVA, $F_{2,12} = 0.77$, $P = 0.655$). Finally, we detected no effect of individual identity on male behaviour (MANOVA, $F_{74,12} = 1$, $P = 0.515$). Escalation behaviours were uncommon (<10% overall) but tended to be used in increasing frequency from the NB to the HB site (c. 4.5% vs. 13.4%). Winners in B-Y dyad contests tended to be B males at the NB (67%) and LB (58%) sites but were equally split between B and Y males at the HB site. Blue males typically won B-O dyad contests at all three sites (NB: 75%; LB: 67%; HB: 100%).

MALE CONDITION AND QUALITY

We found no difference in body condition of males among sites or morphs (ANOVA, site: $F_{2,79} = 2.62$, $P = 0.08$; morph: $F_{2,79} = 0.31$, $P = 0.734$; site \times morph: $F_{4,79} = 1.67$, $P = 0.165$). Lizards differed in the number of bite marks by site (GLM, site: $\chi^2_2 = 7.814$, $P = 0.02$; morph: $\chi^2_2 = 0.805$, $P = 0.669$; site \times morph: $\chi^2_3 = 0.609$,

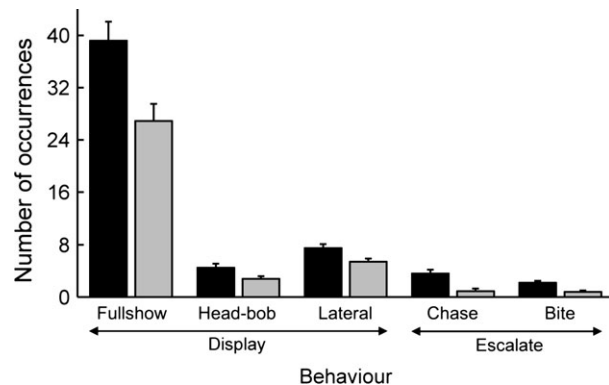


Fig. 5. Behaviours of winning (black bars) and losing (grey bars) male *Urosaurus ornatus* lizards in resource contests ($n = 88$ lizards). Male lizards use display (push-up, head-bob and lateral display) and escalate (chase and bite) behaviours to assert dominance (see Materials and methods). Bars are mean ± 1.0 SE.

$P = 0.894$). Males from the HB site had a greater number of bite marks than males from the NB site (HB site males: 1.7 ± 0.4 bite marks, NB site males: 0.7 ± 0.2 bite marks; $P_{\text{adj}} = 0.048$). Lizards also differed in their ectoparasite load by site, with respect to both mite count (GLM, site: $\chi^2_6 = 19.72$, $P = 0.003$; morph: $\chi^2_6 = 8.94$, $P = 0.177$; site \times morph: $\chi^2_4 = 5.85$, $P = 0.211$) and the number of infested body regions (GLM, site: $F_{2,85} = 4.57$, $P = 0.013$; morph: $F_{2,83} = 0.05$, $P = 0.949$; site \times morph: $F_{4,79} = 1.82$, $P = 0.132$). Lizards at the HB site had fewer mites in fewer body regions compared with lizards at the NB site ($P_{\text{adj}} < 0.001$ and $P_{\text{adj}} = 0.024$, respectively). HB males also had mites in fewer body regions than males at the LB site ($P_{\text{adj}} = 0.038$).

MICROHABITAT USE AND DIET SELECTION

All lizards were captured on or near (<1 m) a live tree or snag. Overall, B males did not vary in microhabitat use across the sites ($\chi^2 = 1.62$, d.f. = 2, $P = 0.445$) and preferred trees over snags (81% vs. 19% overall; $\chi^2 = 16.95$, d.f. = 1, $P < 0.001$). In contrast, Y males shifted to using tree microhabitats at the HB site (79%) relative to the LB (50%) and NB (22%) sites ($\chi^2 = 7.14$, d.f. = 2, $P = 0.028$). Although orange males were consistent in their microhabitat use across sites ($\chi^2 = 5.25$, d.f. = 2, $P = 0.072$), they did not prefer trees or snags ($\chi^2 = 1.33$, d.f. = 1, $P = 0.248$) and were only encountered on snags at the HB site. Overall, males using trees and snags were similar in body size ($F_{1,82} = 0.06$, $P = 0.801$). We detected an interaction between site and perch type ($F_{4,82} = 6.85$, $P < 0.001$). Specifically, males using trees in the HB site were larger than males using trees at the other sites ($P_{\text{adj}} = 0.008$ and $P_{\text{adj}} = 0.01$ for the LB and NB site, respectively).

The patterns of diet selection by B, Y and O males differed by site (Table 2). Overall, all lizards foraged at similar trophic positions at the NB and LB site; however, B males foraged at a higher trophic position than O males

Table 2. Site-specific ANCOVAs of male *Urosaurus ornatus* trophic position, based on carbon and nitrogen stable isotope values of claw tissues. Predictors are morph (blue, yellow or orange) and microhabitat type [living or dead tree (snag)]. Body size [snout-vent length (SVL)] was included as a covariate in these models. Significant *P*-values are italicized

	d.f.	SS	MS	<i>F</i> -value	<i>P</i> -value
NB site					
Morph	2	0.986	0.493	0.71	0.507
Perch	1	1.435	1.435	2.06	0.169
SVL	1	1.224	1.223	1.75	0.202
Morph \times perch	2	2.083	1.042	1.49	0.251
Residuals	18	12.563	0.698		
Low-frequency burn site					
Morph	2	1.295	0.648	0.546	0.587
Perch	1	0.44	0.44	0.371	0.549
SVL	1	0.017	0.017	0.014	0.907
Morph \times perch	2	1.893	0.947	0.799	0.464
Residuals	20	23.705	1.185		
High-frequency burn site					
Morph	2	10.592	5.296	5.79	0.01
Perch	1	5.39	5.39	5.89	0.024
SVL	1	1.129	1.129	1.23	0.279
Morph \times perch	1	0.033	0.033	0.04	0.852
Residuals	21	19.225	0.915		

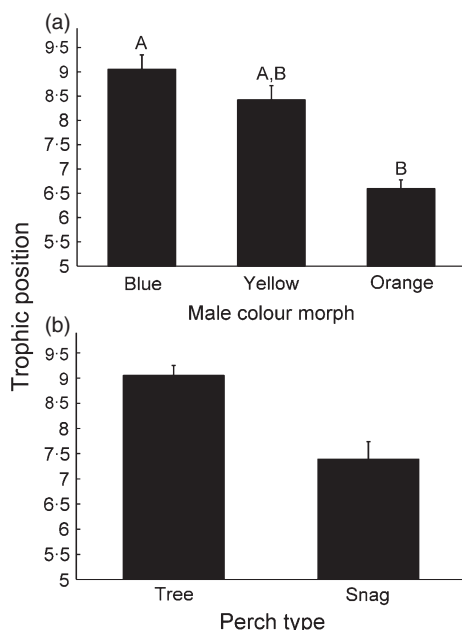


Fig. 6. Trophic position of male *Urosaurus ornatus* at the high-frequency burn site ($n = 29$ lizards). Data are summarized by (a) male colour morph (blue, yellow or orange) and (b) capture site microhabitat [tree ($n = 20$) or snag ($n = 9$)]. Morph sample sizes are provided in Fig. 2c. See eqn 1 in Materials and methods for calculation of trophic position. Letters above bars in (a) denote significant pairwise differences at $\alpha = 0.05$ (see Results). Bars are mean ± 1.0 SE.

at the HB site ($P_{\text{adj}} = 0.008$; Fig. 6a). Lizards captured on trees foraged at a higher trophic position than lizards captured on snags at the HB site (Table 2; Fig. 6b). There was no relationship between body size (SVL) and trophic position (NB site, $r = 0.301$, d.f. = 23, $P = 0.143$; LB site,

$r = 0.004$, d.f. = 25, $P = 0.984$; HB site, $r = 0.336$, d.f. = 26, $P = 0.087$).

Discussion

Animal spatial networks are structured by behavioural interactions between individuals and variability in the abundance of key ecological resources in the environment. Accounting for both of these underlying causes of network variation provides insight into behavioural (Webster *et al.* 2013) as well as ecological (see Results) variation among animal populations (Fig. 1). We investigated these considerations for *U. ornatus* populations inhabiting arid habitats that differ in the frequency of disturbance and environmental quality (Grant *et al.* 2010). Tree lizards establish home ranges and defend territories in live trees (Herrel, Meyers & Vanhooydonck 2001). Because of the variation in tree availability among sites, we expected the lizards to vary in behaviour and resource use. We found differences in network structure and male behaviour across a gradient of resource availability associated with disturbance frequency. A response to resource limitation was the spatial reorganization of morphs in a population in relation to their behavioural differences. Male *U. ornatus* also differed in morphology, body condition and quality among the sites. Furthermore, morph differentiation in microhabitat use and diet may be mediated by the changes in network structure arising as a consequence of disturbance. These factors may favour ecological divergence in resource-limited habitats (e.g. Grant & Grant 2006).

Resource limitation should increase the frequency of competition among individuals for access to preferred microhabitats in resource-rich patches. The patterns of larger male body sizes and greater frequency of combat injuries at the HB site support this prediction. Both age and body size influence competitive ability in lizards (Calsbeek & Sinervo 2002b). Within each study site differences in body size (SVL) among blue, yellow and orange morph *U. ornatus* lizards used in the dyadic contests were negligible. However, across sites, morphs were largest at the resource-limited HB site and had the most injuries (bite marks). Bite marks are an indication of escalation in aggressive behaviour and may lead to permanent scarring, injury or death (Lailvaux *et al.* 2004). Several HB males collected for this study had multiple bite marks on their body (see Fig. S1, Supporting information), and the frequency of chasing and biting during dyadic resource contests was greatest between lizards from the HB site. In contrast, males at the NB and LB sites had zero or one bite mark, indicating that escalated interactions are rare at these sites. Despite evidence for a greater network density and frequency of escalated dominance interactions, lizards at the HB exhibited lower infestations of ectoparasitic mites than males at the other sites. Mites and other parasites can pose serious risks to lizard populations in terms of disease spread and mortality (e.g. Bull, Godfrey

& Gordon 2012; Garrido & Pérez-Mellado 2013). Parasite spread in a population may reflect its spatial network structure (Fenner, Godfrey & Bull 2011) or environmental characteristics (Garrido & Pérez-Mellado 2013). We did not observe differences in infestation among morphs, and infestation was lowest in the most dense network (i.e. at the HB site). Differences in habitat heterogeneity across our study sites may contribute to mite abundance, but more work is needed to investigate this possibility.

The fine-scale shifts in spatial network structure from monomorphic (blue-blue) to polymorphic (blue-yellow) neighbour associations from the NB to HB site appear to have implications for the ecology of *U. ornatus* morphs. Apart from behavioural differences associated with mating success, morphs are assumed to be equivalent in multiple ecological characteristics. However, both behavioural and environmental variations influence the spatial organization of a population and the ability of individuals to exploit preferred resources. Our microhabitat use and diet data support this prediction. Snags represent a poor-quality microhabitat due to their lack of structural heterogeneity and canopy cover. In arid environments, C₃ vegetation types tend to support a greater diversity of arthropods than C₄ vegetation types (e.g. Engle *et al.* 2008). Whereas live trees are embedded within a C₃ (including the tree itself) and C₄ vegetation mosaic, snags are surrounded by C₄ vegetation. At the NB and LB site, only males with blue dewlaps consistently occupied trees, and yellow and orange males exhibited little evidence of habitat selectivity. However, at the HB site, we observed a shift in microhabitat use from snags to trees by yellow males. In contrast, nomadic orange males were only encountered on snags at this site. We also detected trophic divergence among the morphs at the HB site. Trophic niche differentiation may enhance rates of speciation, especially in polymorphic species such as *U. ornatus* (Skúlason & Smith 1995). The trophic positions of blue and yellow males, both of which occupied trees, were higher than the position of orange males, which occupied snags. In these grasslands, foraging at a high trophic position involves greater consumption of beetles and spiders over herbivorous arthropods (M. S. Lattanzio & D. B. Miles, in review). Predatory arthropods are protein rich (Wilder *et al.* 2013) and may represent high-quality, preferred prey to an insectivore (e.g. Blanco, Laiolo & Fargallo 2014). In contrast, greater vegetation heterogeneity may mask morph differences in diet at the NB and LB sites. The microhabitat use and diet variation documented in our study represent underappreciated ecological consequences of a colour polymorphism.

The male colour polymorphism in *U. ornatus* is associated with alternative mating strategies likely maintained by a combination of negative frequency-dependent and socially mediated selection (Sinervo, Bleay & Adamopoulou 2001). Variation in the patterns of morph integration into a spatial network may thus affect the relative success of each morph's strategy (e.g. Sih, Hanser & McHugh

2009). For example, in small polymorphic populations, demographic stochasticity may favour usurpers over territory defenders because of the greater variance in usurper mating success (Calsbeek *et al.* 2002). Similarly, when the availability of preferred microhabitats for establishing territories is limited (see Table S1, Supporting information), usurpers may experience a fitness advantage because fewer territorial (e.g. blue) males will be supported in the population and territorial exclusion among those males should be favoured to minimize resource competition (e.g. Talents *et al.* 2012). Yellow morph *U. ornatus* typically exhibits a satellite mating tactic, but our data reveal that they are also capable of aggressive behaviour when interacting with blue males. Yellow males were often winners of these contests (c. 33–50% of contests, see Results), especially between males originating from the HB site. Usurpation may be a successful tactic in the wild, especially in resource-limited habitats. Fewer preferred territories (live trees) at the HB site may then favour an increase in yellow morph frequency (i.e. due to greater reproductive success, Calsbeek *et al.* 2002). Multi-year capture data support that at our study sites yellow morph males are present in greater proportions than other morphs in burned sites (see Fig. 2) (percentage of males that are yellow morph in 2010: LB, 46.2%; HB, 37.5%; and in 2011: LB, 47.1%; HB, 43.5%; M. S. Lattanzio & D. B. Miles, unpublished data). More work is needed however to determine whether yellow males sire more offspring than other morphs in burned sites.

Conclusions

A major goal of ecology is understanding how individual variation in behaviour structures social systems among populations that inhabit disparate environments. However, this connection also requires quantifying how behavioural variation (e.g. Pike *et al.* 2008) influences suites of physiological and ecological traits that affect mating behaviours (e.g. alternative mating strategies, Sinervo & Lively 1996) and fitness. We applied network theory in relation to potential mating strategy as evidenced by dewlap colour (Sinervo & Lively 1996; Moore, Hews & Knapp 1998). We show that environmental variation perturbs the spatial dispersion of morphs in only certain contexts and that this perturbation may have social, ecological and fitness ramifications (e.g. Fig. 1). For species such as *U. ornatus*, these effects may then feed back into patterns of reproductive success among the morphs, affecting the maintenance of colour polymorphism across the species' range.

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Data accessibility

The data used in this study are archived in the Dryad digital repository: <http://doi.org/10.5061/dryad.r37rm> (Lattanzio & Miles 2014).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Examples of bite marks on male *U. ornatus* lizards.

Table S1. Relative cover and isotopic characteristics of vegetation at the study sites.

Table S2. Summarized mark–recapture data for male lizards at the study sites.

Table S3. Description of *U. ornatus* spatial networks at the study sites.