# EFFECTS OF VEGETATION DENSITY ON HABITAT SUITABILITY FOR THE ENDANGERED GREEN AND GOLDEN BELL FROG, *Litoria Aurea*

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Abstract.—Habitat offsetting is a conservation management regime used to preserve biodiversity when human development degrades areas inhabited by threatened species. Habitat suitability of a threatened species can vary temporally due to environmental changes. However, vegetation growth is rarely considered prior to mitigation attempts. The Green and Golden Bell Frog (Litoria aurea) is threatened by habitat loss and has been the subject of several habitat offsetting projects. Despite following recommended habitat templates, nearly all management projects have failed in creating a self-sustaining population. In this study, we examined differences in L. aurea occupancy among ponds with varied levels of vegetation density. We investigated extant occupancy patterns during a 2-y period among areas of sparse, medium, and dense vegetation growths. We also conducted a field manipulation experiment to determine differences in abundance and biotic and abiotic factors between waterbodies with either sparse (manually removed) or dense (naturally overgrown) vegetation covers. Occupancy by adult females and juveniles, but not adult males, differed among sites with different vegetation densities. Female occupancy was greater at sites with medium vegetation densities; whereas, juveniles occupied medium and densely vegetated waterbodies more frequently than sparsely vegetated waterbodies. We also detected differences in potential predators, aquatic competitors, food resources, and water quality between the sparsely and densely vegetated waterbodies. Our data should allow for better habitat management of future L. aurea compensatory projects, and underscores the importance of using both quantitative and qualitative pre-analysis to question temporal variances in habitat suitability prior to management offsets.

Key Words.--adaptive management; conservation management; disturbance; habitat offset; succession; vegetation growth

#### INTRODUCTION

As modification of environmental landscapes reduce the biodiversity value of many habitats, protected ecological areas such as national parks, wilderness areas, and biosphere reserves increase in importance. Often there are too few of these protected areas to sufficiently support threatened species and as such, the need for habitat creation and active management is growing (Madsen et al. 2010; Quintero and Mathur 2011; Maron et al. 2012). Created habitats can be suboptimal or may become so over time, resulting in population declines of many target species (Dennis et al. 2011). The effectiveness of compensatory projects oftentimes is questionable because of a lack of either on-going management or understanding of habitat requirements, with little consideration of stochasticity and temporal change in habitat quality (Matthews and Endress 2008; Maron et al. 2012).

An often-overlooked aspect in conservation management is how vegetation growth and succession affect habitat suitability (Walker et al. 2007). The results of numerous compensatory efforts highlight the critical impacts that altered vegetation coverage can have. For example, an attempted re-introduction of the Cheer Pheasant (Catreus wallichi) to the Margalla Hills National Park in Pakistan was unsuccessful because of the conversion of a habitable, sparsely vegetated environment to a dense impenetrable shrubland (Garson et al. 1992). Similarly, reintroductions of orthoptera species richness to grassland habitats in Europe correlates with vegetation densities, with lowest species richness occurring in habitats with dense vegetation and highest in habitats with moderate amounts of vegetation (Fartmann et al. 2012). Reintroduced populations of the Stitchbird (Notiomystis cincta) of New Zealand flourish in pristine densely vegetated habitats, but diminish in disturbed and sparsely vegetated habitats because of growth of a fungus in these areas (Perrott and Armstrong 2011). Such evidence highlights the importance of considering changes in vegetation density in the context of habitat suitability to successfully offset impacts of habitat disturbance (Matthews and Endress 2008; Maron et al. 2012).

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In Australia, the Green and Golden Bell Frog (Litoria aurea) is a threatened species impacted by habitat loss and is the subject of several compensatory habitat initiatives (Daly 1996; Pyke et al. 2008; Stockwell et al. 2008; Pickett et al. 2013; Valdez et al. 2017a). Litoria aurea is a generalist species that frequently inhabits disturbed environments in urban or industrialized areas (Pyke and White 2001; Mahony et al. 2013; Valdez et al. 2015). This species commonly occupies ephemeral ponds and early successional stages of ponds, such as newly created flooded scrapes, both of which have little to no vegetation when compared to permanent ponds (Pyke and White 1996). Most management strategies for L. aurea have actively involved a disturbance regime based on observed habitat associations (Sydney Olympic Park Authority [SOPA] 2002). However, past L. aurea compensatory attempts have had poor outcomes (Daly et al. 2008; Pyke et al. 2008; Mahony et al. 2013; Klop-Toker et al. 2016; Valdez et al. 2017a), and the effects of vegetation density on suitability of habitat for L. aurea has yet to be tested directly.

In this study, we examine the effects of vegetation density on L. aurea habitat use. We do this by identifying whether occupancy by an extant population of L. aurea during a 2-y period reflected selection for a habitat of particular vegetation density, and by determining differences in abundance of L. aurea, potential predator, prey and competition abundances, and abiotic factors between sparse and dense vegetation covers in a field experiment. We hypothesize that vegetation density affects occupancy and abundance of L. aurea. Based on the low success rate of compensatory efforts, which predominantly established sparsely vegetated habitats for this species, we predict that increased vegetation density will increase L. aurea occupancy and abundance. The outcomes from this study will help inform future compensatory efforts for this species and perhaps serve as a guide for other threatened species.

#### **MATERIALS AND METHODS**

Study site.—The study site was the deltaic Kooragang Island in the Hunter region of New South Wales, Australia ( $32^{\circ}51'13.11''S$ ,  $151^{\circ}42'41.48''E$ ), which is inhabited by one of the largest remaining extant populations of *L. aurea* (Hamer and Mahony 2010). Various habitats are present on the island, including salt marshes, mangroves, freshwater wetlands, remnant forests, and wet pastures (Day et al. 1999). Human activities altered the landscape and hydrology for agricultural and industrial purposes, but the northern area is now reclaimed as a national park and currently is a nature reserve within the Hunter Wetlands National Park system. The southern area of the island is still heavily

industrialized and contains coal loading facilities for the Port of Newcastle.

**Data collection**.—To model *L. aurea* occupancy, we surveyed 52 natural ponds (20 permanent, 17 semipermanent, and 15 ephemeral) within industrial and national park areas. The percentage cover of emergent aquatic vegetation (e.g., Bullrush, *Typha orientalis*, Common Reed, *Phragmites australis*, Water Ribbon, *Triglochin procerum*, and Bulrush, *Scheonoplectus littoralis*) varied among the ponds from 0% to 100%. We measured the percentage cover of aquatic vegetation at the start of each season, and categorized the vegetated habitats of ponds as sparse (66–100% open water), medium (33–65% open water), or dense (0–32% open water) based on the percentage of open water present.

To determine occupancy of *L. aurea* during the 2011–2012 and 2012–2013 breeding seasons (the austral spring to summer), we conducted timed visual encounter surveys (VES; Crump and Scott 1994) once a month at the first 2–4 h of darkness (nocturnal surveys) and the first 2–6 h of light (diurnal surveys). During each survey, we inspected the ground, water, and vegetation in each pond, starting at the perimeter and walking slowly and quietly inwards looking both up and down until the entire pond had been searched. We recorded the time taken to complete the survey to compare search effort and observations between the pond area surveys.

Following VES, we captured *L. aurea* by hand. Our hands were covered in a disposable plastic bag, which we then inverted and tied closed to contain the frog. We measured, weighed, determined the sex, estimated age class (e.g. adult or juvenile), and recorded the location of all individuals using GPS. We classified frogs  $\geq 45$ mm snout to vent length (SVL) as adults and those < 45 mm SVL as juveniles (Hamer and Mahony 2007). We identified males by the presence of nuptial pads (a dark mark along the inner finger) and females as adults without nuptial pads (Hamer and Mahony 2007).

**Occupancy models.**—We used Robust Design occupancy models in the program MARK (version 6.1; MacKenzie et al. 2003) to estimate the parameters of occupancy probability ( $\Psi$ ), extinction probability ( $\epsilon$ ), and detection probability (p) among open, medium, and densely vegetated ponds. We developed a set of models for all *L. aurea* combined and for juveniles, males, and females independently, with each parameter modeled to be either constant (.) or a function of the vegetation cover (g; sparse, medium or dense). We also modeled occupancy and detection probabilities as an interaction between vegetation cover and time (month and year). To ensure that all the influential factors were considered in each independent analysis, we derived all parameter



FIGURE 1. Treatment plots of (A) Sparse vegetation cover treatment area in which vegetation has been removed from the interior  $4 \times 4$  m, leaving a surrounding emergent aquatic vegetation buffer of 1 m; (B) A neighboring dense vegetation cover control of dense emergent aquatic vegetation. (Photographed by Loren Fardell).

estimates and standard errors by model averaging (Burnham and Anderson 2002). Finally, we compared occupancy probabilities between the vegetation covers using the Error Bars Overlap Rule, where a < 50% overlap corresponded to a  $P \le 0.05$  level of significance (Cumming et al. 2007).

Field experiment.-We chose previously occupied densely overgrown ephemeral swale habitats from three locations in the Hunter Wetlands National Park area on Kooragang Island. We selected these sites based on observations during the past 20 y that had shown a decline in L. aurea. For the purposes of this study, we created a sparse vegetation cover by clearing dense vegetation growth, of predominantly T. orientalis and grass species in a  $4 \times 4$  m area with a surrounding 1 m emergent edge vegetation buffer left in place (Fig. 1). We also identified a neighboring habitat covered with dense vegetation as a  $5 \times 5$  m area that was naturally overgrown with predominantly T. orientalis. We chose a total of 26,  $5 \times 5$  m experimental plots within the three locations and divided them into either sparse or dense treatments paired in a single line checkerboard design (n = 13 for each; Fig. 2).

We conducted surveys once every two weeks from January to May during the 2013 breeding season to determine *L. aurea* abundance using diurnal surveys timed VES to locate and estimate the age class of each individual frog encountered (we did not capture or measure the frogs). To detect chorusing males, we conducted nocturnal surveys using a portable audio device with speakers to play a pre-recorded call of *L. aurea* at the edge of each pond.

We also conducted visual surveys every two weeks to determine the presence (direct sightings or scats) of potential predators (e.g., skinks, snakes, and rodents), competitors, and food resources. We used ink tunnels (Pest Control Research, Rolleston, Christchurch, New Zealand) to capture foot prints of all animals. In each plot, we secured two tunnels either to vegetation just above the water line or on the ground if dry. We detected terrestrial invertebrates using blue and yellow sticky insect traps (Bugs for Bugs, Mundubbera, Queensland, Australia) by securing one trap of each color per plot to vegetation approximately 100 cm above the water line. We also used dip nets to capture aquatic invertebrates and vertebrates to determine abundances, and to quantify detritus by the percentage of the net filled. Additionally, we dip-netted systematically with five continuous zigzagged sweeps using a 40 cm Ø net of  $0.9 \times 0.3$  mm mesh size. We also submerged and randomly positioned two terracotta (roof) tiles in each plot to determine the percentage cover of algae growth over time. Lastly, we haphazardly placed two sticky insect traps and ink tunnels per plot into position on the first survey occasion, and replaced them every two weeks with new traps in the same location.

We measured weather and water quality to determine differences between the sparse and dense vegetation covered ponds. At the end of each diurnal survey, we walked out to the center of each pond and recorded weather measurements using a Kestrel 3500 hand-held weather meter (Kestrel Meters, Minneapolis, Minnesota, USA), holding the meter approximately 100 cm above the water surface. We recorded temperature, relative humidity, heat index (apparent temperature), dew point (minimum temperature that water droplets may condense), wet bulb (temperature pocket of air would have at saturation point), wind chill, and wind speed. Furthermore, we recorded water quality measurements, such as temperature, dissolved oxygen, pH, salinity, resistance, conductivity, and total dissolved solids, using a Professional Plus Quarto water quality probe meter (YSI Inc., Yellow Springs, Ohio, USA) at the start of each diurnal survey at approximately 100 cm from the edge of the plot (at the same position each survey).

*Statistical analysis.*—To identify differences in biotic and abiotic parameters between sparse and dense vegetation covered ponds, we conducted Welch's unequal

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FIGURE 2. Aerial view of Kooragang Island, New South Wales, Australia, showing numbered ponds 1 to 26 used to study Green and Golden Bell Frogs (*Litoria aurea*). Each red square represents a  $5 \times 5$  m pond area. Even numbered ponds were cleared of vegetation to a sparse cover, and odd numbered ponds were left as dense vegetation covers. (Image taken from Google Earth, 2017).

variances *t*-test, which is robust to deviations from normality and provides a better control of Type I Error rates than alternative parametric and nonparametric tests (Skovlund and Fenstad 2001; Fagerland and Sandvik 2009; Delacre et al. 2017). To correct for family-wise error rate (the probability of at least one Type I Error), we used sequential Bonferroni correction for each group (climate, water, predators, competitors, food resources; Cabin and Mitchell 2000). We conducted all tests with the program R, version 3.4.2 (R Core Team 2015).

## RESULTS

**Occupancy**.—During the survey period, we did not detect any extreme weather events (e.g., floods or droughts) that would have abnormally altered *L. aurea* occupancy or detection. From the 52 ponds surveyed, we detected *L. aurea* in 11 ponds during 2011–2012 and in 16 ponds during 2012–2013. We found *L. aurea* at least once in only 32% of sparsely vegetated ponds (n = 34), compared to 50% in both medium (n = 10) and densely vegetated ponds (n = 8).

For the occupancy modeling, we found multiple models were reasonable with no top-model (with

weighting of 90–100) evident (Table 1). The estimated probability of extinction between the two survey periods was constant (81% for all, 84% for juveniles, 92% for males, and 0.05% for females) as was the averaged probability of the capture of an individual between the three habitat densities (51% for all, 41% for juveniles, 52% for males, and 38% for females). There was no difference between occupancy between the three vegetation densities and between *L. aurea* sex and age classes (Fig. 3).

The most parsimonious models for occupancy probability ( $\Delta$ AICc difference < 2) for all *L. aurea*, juveniles, males, and females included occupancy as a constant and did not vary with the level of vegetation density and pond openness (group) or between the months and years (time; weights of 74%, 51%, 79%, and 45%, respectively; Table 1). For both the juveniles and the females, there was a second most parsimonious model that modeled occupancy as a function of the vegetation density and the year of the survey (weights of 35% and 29%, respectively; Table 1). The model average estimate for probability of occupancy by all *L. aurea* in each of the vegetation density habitats was similar between the habitats and between the

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**TABLE 1.** Models for all Green and Golden Bell Frogs (*Litoria aurea*) combined, for juveniles, males, and females ranked by ascending  $\Delta$ AICc, used to estimate occupancy probability ( $\Psi$ ), including the parameters of extinction probability between primary survey periods (E) and the probability of detection (P). Each parameter was modeled as a constant (.), or as a function of the grouping (g) by vegetation density and pond openness (sparse, medium, and dense), or as a function of this grouping between the time periods of year or month and year. The table includes Akaike's Information Criterion corrected (AICc),  $\Delta$ AICc for model selection, weight (*w*) in favor of each model having the best fit, and the number of parameters.

	Model	AICc	ΔAICc	weight (w)	No. of parameters
Combined	Ψ(.)Ε(.)Ρ(.)	283.18	0.00	0.74	3
	Ψ(g)E(.)P(.)	286.54	3.36	0.14	5
	$\Psi(g^*year)E(.)P(.)$	287.32	4.15	0.09	8
	$\Psi(g^*year)E(g)P(.)$	289.67	6.50	0.03	10
	$\Psi(g^*year)E(g)P(g)$	293.52	10.35	0.00	12
	$\Psi(g^*year)E(g)P(g^*year)$	302.23	19.05	0.00	15
	$\Psi(g^*year)E(g)P(g^*month^*year)$	314.74	31.56	0.00	28
Juveniles	Ψ(.)E(.)P(.)	180.56	0.00	0.51	3
	$\Psi(g^*year)E(.)P(.)$	181.33	0.77	0.35	8
	Ψ(g)E(.)P(.)	183.83	3.27	0.10	5
	$\Psi(g^*year)E(g)P(.)$	185.80	5.24	0.04	10
	$\Psi(g^*year)E(g)P(g)$	190.73	10.17	0.00	12
	$\Psi(g^*year)E(g)P(g^*year)$	195.55	14.99	0.00	14
	$\Psi(g^*year)E(g)P(g^*month^*year)$	208.88	28.33	0.00	27
Males	Ψ(.)E(.)P(.)	219.72	0.00	0.79	3
	Ψ(g)E(.)P(.)	222.74	3.02	0.18	5
	$\Psi(g^*year)E(.)P(.)$	226.35	6.64	0.03	8
	$\Psi(g^*year)E(g)P(.)$	230.00	10.29	0.00	10
	$\Psi(g^*year)E(g)P(g^*year)$	236.12	16.41	0.00	14
	$\Psi(g^*year)E(g)P(g)$	236.43	16.71	0.00	12
	$\Psi(g^*year)E(g)P(g^*month^*year)$	282.54	62.81	0.00	32
Females	Ψ(.)E(.)P(.)	188.11	0.00	0.45	3
	$\Psi(g^*year)E(.)P(.)$	188.99	0.89	0.29	8
	Ψ(g)E(.)P(.)	190.10	2.00	0.17	5
	$\Psi(g^*year)E(g)P(.)$	191.40	3.30	0.09	9
	$\Psi(g^*year)E(g)P(g)$	196.10	7.99	0.01	11
	$\Psi(g^*year)E(g)P(g^*year)$	197.99	9.88	0.00	13
	$\Psi(g^*year)E(g)P(g^*month^*year)$	222.08	33.97	0.00	26

2011–2012 and 2012–2013 surveys (Fig. 3a). The model average estimate for probability of occupancy for both the females and the juveniles was higher in the medium vegetation density habitats between the first survey season and in the sparse vegetation (47.44% and 42.08% overlap, respectively; Fig. 3b and d) and in dense vegetation habitats for the juveniles between the second survey season (42.08% overlap; Fig. 3d). For males, occupancy was consistent between each vegetation density for both seasons (Fig. 3c).

*Field experiment.*—During the three initial survey periods (January to early February) all ponds were dry, but by the fourth survey period (mid-February), all of the 26 ephemeral ponds had naturally flooded with rainfall.

Therefore, we replicated the water measurements seven times instead of 10. We observed 21 *L. aurea*, with nine adults (four in sparse and five in dense vegetated ponds) and 12 juveniles (two in sparse and 10 in dense vegetated ponds). There was no significant difference of total *L. aurea* observed per minute, or adults observed between the sparse and densely vegetated habitats (P = 0.100, CI 0.16–1.17; and P = 0.776, CI 0.20–3.27, respectively). Juvenile occupancy was significantly different between the sparse and dense vegetated ponds, with an average 79% fewer in the sparsely vegetated habitats (mean ratio of sparse/dense = 0.21, P = 0.048, CI 0.04–0.99).

We found the observed presence of several predators including skinks and snakes were equal between the two vegetation densities. However, there were significant





**FIGURE 3**. Occupancy probability of the Green and Golden Bell Frog (*Litoria aurea*) among three vegetation densities and pond openness categories (sparse, medium, dense). The occupancy probabilities were predicted by models of the total *L. aurea* present (A), the presence of juveniles (B), the presence of males (C), and the presence of females (D) between 2011–2012 (Yr1) and 2012–2013 (Yr2). Error bars are 95% confidence intervals. Asterisks (\*) represent  $P \le 0.05$ .

differences in the observed presence of other possible predators: aquatic beetles, rodents, and other terrestrial animals. Aquatic beetles were more abundant in the sparsely vegetated ponds compared to the densely vegetated (Table 2; Fig. 4). Moreover, rodent activity and animal bites were more frequent in the densely vegetated ponds compared to the sparsely vegetated ponds (Table 2; Fig. 4).

**TABLE 2.** Mean differences in biotic and abiotic factors between waterbodies supporting Green and Golden Bell Frogs (*Litoria aurea*) with either sparse (manually removed vegetation) or dense (naturally overgrown) vegetation covers. *P* values (\* P < 0.05, \*\* P < 0.01, \*\*\* P < 0.001) from Welch's unequal variances *t*-test and adjusted for multiple tests with the sequential Bonferroni correction.

Parameter	Dense	Sparse	P value
Aquatic beetles	4.33	8.96	***
Rat tracks	25.5	14.9	***
Animal bites	0.93	0.72	**
Water boatmen	0.61	4.57	***
Snails	0.50	1.08	*
Other tadpoles	1.49	3.75	*
Detritus	23.7	66.8	***
pН	6.11	5.99	**

We found the abundances of several competitors including other frog species and aquatic organisms were equal between the two vegetation densities. There were higher abundances of the potential competitors in the aquatic areas of the sparsely vegetated ponds such as water boatmen (Corixidae), aquatic snails, and tadpoles of other species (Table 2; Fig. 5). We identified tadpoles as those of the Eastern Dwarf Tree Frog (*Litoria fallax*) and the Striped Marsh Frog (*Litonodynastes peronii*).

We found the abundances of several food resources, including algae and aquatic spiders and the diversity of insect orders, were equal between the two vegetation densities. Aquatic detritus was significantly higher in the sparsely vegetated ponds (Table 2; Fig. 5). The weather variables did not differ between the sparsely vegetated and the densely vegetated ponds. Similarly, most of the water quality variables did not differ between the two vegetation densities. However, we found significant differences in pH between vegetation densities (Table 2).

## DISCUSSION

The effect of habitat decline and degradation on biodiversity has garnered enough concern that habitat



FIGURE 4. The raw data averages for the abundances of aquatic beetles (A) and rat tracks (B) compared between the dense and sparse vegetated habitats. Error bars are one standard error of the dense (black dotted lines) and the sparse (red lines) raw data averages.



FIGURE 5. The raw data averages for the abundances of water boatmen (Corixidae; A), aquatic snails (B), other tadpole species (C), and aquatic detritus (D) compared between the dense and sparse vegetated habitats. Error bars are one standard error of the (black dotted lines) and the sparse (red lines) raw data averages.

offsetting regimes are increasingly implemented when human developments are proposed (Madsen et al. 2010; Germano et al. 2015). Offsetting management programs in new locations should question whether this creates the optimum habitat for a threatened species and how temporal changes may affect habitat suitability (Madsen et al. 2010; Quintero and Mathur 2011). Vegetation growth in density is an important factor in habitat quality and understanding its affects will improve the success of these management programs. This would allow for an avoidance of any possible negative effects, due to limitations of habitat structural diversity and reduce the threat of biodiversity loss. Investigating habitat suitability prior to the implementation of an offsetting project is, therefore, important as it can improve decision making and reduce uncertainties.

Our data did not support the prediction that increased vegetation increases abundance and occupancy of all *L*.

aurea, although adult females and juveniles occupied medium vegetated habitats in greater abundances than males, which occupied all vegetation densities similarly across the survey seasons. However, we did not find a difference in occupancy and abundance for any sex or age class during the second season, which may be explained by a breeding event and the subsequent dispersal behavior from the natal ponds during this period (Pyke and White 2001). Our data further reveals differences in juvenile occupancy between the sparse and dense vegetation, with greater occupancy in the densely vegetated structures. These results are consistent with recent findings that juveniles prefer aquatic vegetation compared to open water (Valdez et al. 2016). Because juveniles are more vulnerable to predation threats, their greater abundance in dense vegetation is likely associated with shelter refuges and available food resources (Goldingay and Lewis 1999; Pyke and White 2001; Hamer et al. 2002; Goldingay 2008; Bower et al. 2013).

The sparsely vegetated habitats contain higher levels of the potential food resources of aquatic detritus, which could provide positive growth support for L. aurea (Bower et al. 2013). Moreover, sparsely vegetated habitats contain fewer predatory animals, such as rodents and other terrestrial animals, which decreases survival rates and population densities of L. aurea (White and Pyke 2008). Sparsely vegetated habitats also have greater abundance of competitors and predators of L. aurea: water boatmen (Corixidae; Resh and Cardé 2003), aquatic snails (Brönmark et al. 1991; Cogger 2000), and aquatic beetles (Resetarits and Wilbur 1989). Other tadpole species are also more abundant in the sparse vegetation, which may be explained by the lower pH that is more favorable to tadpole growth (Horne and Dunson 1995; Angilletta et al. 2004; Smith et al. 2007). This is important because interspecific competition among tadpoles results in decrease immune fitness in post-metamorphic individuals (Clulow et al. 2015) and increases the probability of site extinction (Valdez et al. 2015). Moreover, some amphibians avoid breeding at sites inhabited by tadpoles of other species (Resetarits and Wilbur 1989; Petranka et al. 1994).

Contrary to a previous assumption (Pyke and White 1996), our data suggest that juveniles and females occur in greater abundances in moderately vegetated habitats than sparsely vegetated sites. Therefore, it may be inferred that compensatory management regimes for this threatened species should allow for a certain level of vegetation growth in density, instead of implementing regular disturbance regimes, as previously suggested. Nevertheless, other types of habitat besides vegetation are also required, such as mimicking proportions similar to those in the natural landscape (Valdez et al. 2017b). The best approach for future management regimes is to allow for a mosaic of both sparse and dense vegetated habitats, so that appropriate densities may be used to find the optimum niche considering other influential variables.

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