



Density of an environmental weed predicts the occurrence of the king brown snake (*Pseudechis australis*) in central Australia

Peter J. McDonald^{1,2} & Gary W. Luck³

¹Flora and Fauna Division, Department of Land Resource Management, Northern Territory Government, Alice Springs, NT, Australia,

²School of Environmental Sciences, Charles Sturt University, Albury, NSW, Australia,

³Institute for Land, Water and Society, Charles Sturt University, Albury, NSW, Australia

The king brown snake (*Pseudechis australis*) is a large and highly venomous elapid, which occurs throughout much of mainland Australia. Although an ecological generalist, anecdotal evidence suggests that individuals in the arid-zone are more frequently observed in proximity to dense grass cover. We tested the hypothesis that *P. australis* are more likely to be located close to dense grass cover in an arid region near Alice Springs in the Northern Territory. We focused on the environmental weed buffel grass (*Cenchrus ciliaris* L.) because this species comprises the highest density of cover in the region. Under an Information-Theoretic framework we used logistic regression to model the occurrence of *P. australis* against a range of habitat variables expected to influence the snakes distribution and abundance. There was substantial support for our hypothesis with the model including only the variable buffel grass as the best ranked model predicting *P. australis* presence. The probability of recording *P. australis* in a location increased with the density of buffel grass cover. Eradicating or reducing buffel grass in and around built-up areas may reduce the risk of interactions between humans or domestic animals and *P. australis*.

Key words: elapid, habitat, snake, venomous

INTRODUCTION

The king brown or mulga snake (*Pseudechis australis*) is a large (SVL up to 2.3 metres), heavily-built and highly venomous elapid (Elapidae) distributed throughout much of mainland Australia (Shine, 1987; Wilson & Swan, 2010; Fig. 1). It is regarded as an ecological generalist; occurring in habitats ranging from tropical woodlands in the northern parts of its range to arid spinifex deserts in the south and feeding on a variety of terrestrial vertebrate prey (Shine, 1987; Wilson & Swan, 2010). Although considered as a habitat generalist, anecdotal evidence suggests that arid-dwelling *P. australis* are more frequently observed in proximity to dense grasslands, particularly when these grasslands occur in riparian habitats (Orange, 2009; PM pers. obs.).

Buffel grass (*Cenchrus ciliaris* - nomenclature according to Albrecht et al., 1997) is an exotic perennial tussock grass (originally from Africa and south-west Asia) deliberately established throughout Australia's arid zone as pasture for cattle and as a soil stabilizer (Smyth et al., 2009). Since its introduction in the late 1800s, the grass has spread throughout the northern and central regions of arid Australia and is now regarded as a serious environmental weed (Eyre et al., 2009).

The highly invasive species readily out-competes native vegetation, frequently forming dense swathes where native vegetation had previously been sparse or only seasonally dense (e.g., rainfall-triggered growth of native tussock grasses and forbs) (Clarke et al., 2005; Miller et al., 2010; Fig. 1). Although buffel grass tends to favour and more readily colonize 'run-on' landforms (e.g., floodplains), it is increasingly adapting to and spreading in less productive areas (Smyth et al., 2009; Miller et al., 2010).

Given the continuing spread of buffel grass throughout arid Australia, the propensity for it to form dense stands, and the possible association between *P. australis* occurrence and grass density, we suggest that buffel grass may be an important environmental factor influencing the distribution and abundance of the snake species. Our hypothesis is that the probability of occurrence of *P. australis* will increase with increasing buffel grass density. Such an association has substantial implications for the safety of humans and domestic animals in arid regions, given that *P. australis* is a highly venomous and dangerous species (Currie, 2004). Hence, the way buffel grass is managed may have major implications for the outcomes of human-snake and domestic animal-snake interactions

MATERIALS AND METHODS

Our study was conducted in the MacDonnell Ranges bioregion which covers 39,300 km² of upland in the southern Northern Territory (NT), Australia (see McDonald et al., 2012 for a description of the landforms and land-uses of the area). We used systematic road-cruising (Rosen & Lowe, 1994) to sample *P. australis* along a 77 km sealed road transect which included part of Namatjira Drive (23°48'33"S, 133°13'16"E to 23°40'1"S, 132°38'8"E) and all of the Ormiston Gorge access road (23°41'5"S, 132°42'34"E to 23°37'57"S, 132°43'39"E) west of the town Alice Springs (Fig. 1). This transect runs through a range of habitat types typical of the bioregion (see McDonald et al. 2012 for a map illustrating the typical mosaic of vegetation communities that occurs along the road transect), including areas with varying levels of buffel grass infestation. One of us (PM) drove this transect on 77 nights over a 12 month period between August 2009 and July 2010. Each night the transect was driven twice (two laps) at a speed of 40–60 km/hr, with the transect start point alternated between the east and west ends. The location of all *P. australis* individuals encountered was marked with a hand held GPS. All live animals were caught, individually marked by scale clipping (Brown & Parker, 1976) and released on the road verge adjacent to the point of capture. Road-kill animals were removed from the road surface.

In order to test whether there was an association between buffel grass density and *P. australis* occurrence in our study area, we modelled data under an Information-Theoretic framework (Burnham et al., 2011). This involved developing a set of *a priori* hypotheses (models) to explain variation in the response variable (snake presence/absence) based on consideration of existing knowledge from the literature and/or field experience (Burnham et al., 2011). Models were then compared to identify the best explanation (among the

set of models considered) of variation in the response variable. Using information from the literature and our own field observations, we developed a set of models to explain the occurrence of *P. australis* that included variables with the potential to influence the distribution or abundance of the species (see Table 1 for justification for variable inclusion). Relevant variables were recorded within a 50 m radius around each location where a snake was encountered and a single proximity variable (distance to major drainage) was also recorded (Table 1). All variables were also recorded at 50 randomly selected locations where the snake species was absent along the road transect. The randomly selected locations were a minimum of 500 m from the nearest *P. australis* presence location and can be referred to as 'pseudo absences' (Milne et al., 2005).

We initially tested for collinearity among the independent (predictor) variables using the Spearman correlation coefficient. Because no pair of variables exhibited a correlation coefficient of greater than 0.6, no variable was removed from further analysis (McDonald et al., 2012). We further checked for multi-collinearity among the independent variables by regressing each independent variable against all the others using linear regression and examining the values of the variance inflation factors. In these analyses, all variance inflation factor values were less than 2 indicating very low levels of multi collinearity (see Zuur et al., 2010).

All variables were modelled using binary logistic regression, with presence (1) or absence (0) as the dependent variable. We also modelled combinations of independent variables where these combinations made biological sense (e.g., RIPAR_50 + MAJDRAIN_DIST). Models were ranked using Akaike's Information Criterion corrected for small sample size (AIC_c). This is appropriate when the number of data points/maximum number of fitted parameters is less than 40 (Symonds & Moussalli, 2011). Models with smaller values of AIC_c have greater

Table 1. Habitat variables recorded at presence and pseudo-absence locations for *Pseudechis australis*

Variable	Description	Method of data collection	Biological knowledge of <i>P. australis</i>
MAJDRAIN_DIST	Distance (m) to nearest major drainage line, identified by presence of River Red gums (<i>Eucalyptus camaldulensis</i>)	Google Earth ¹	Encountered more frequently in close proximity to alluvial systems (floodplains, rivers, creeks) ^{a, b}
RIPAR_50	% area of riparian woodland/grassland within a 50 m radius of sample site	Field survey ²	Encountered more frequently in close proximity to alluvial systems (floodplains, rivers, creeks) ^{a, b}
BUFF_COVER	% area of <i>Cenchrus ciliaris</i> cover within a 50 m radius of sample site	Field survey ²	Encountered more frequently in close proximity to dense grassland ^b
TUSSCK_COVER	% area of native soft grass (e.g. <i>Aristida</i> pp.) cover within a 50 m radius of sample site	Field survey ²	Encountered more frequently in close proximity to dense grassland ^b
HUMCK_COVER	% area of native hummock grass (<i>Triodia</i> spp.) cover within a 50 m radius of sample site	Field survey ²	Encountered more frequently in close proximity to dense grassland ^b

References: ^aPM pers. obs., 2005–2010; ^bOrange, 2009; Methods: ¹Distance tool used on Google Earth Pro, with major drainage lines clearly visible on SPOT-derived satellite imagery; ²On-ground survey with measurements of habitat made by visual estimation

Table 2. AIC_c ranked models explaining the occurrence of *Pseudechis australis* in the study area

Model (coefficient; standard error) ^a	AIC_c	Δ_i	w_i	Hosmer and Lemeshow test	
				χ^2	p
BUFF_COVER (0.06; 0.02)	100.41	0.00	0.31	2.60	0.75
RIPAR_50 (0.01; 0.01) + BUFF_COVER (0.04; 0.02)	100.81	0.40	0.25	4.00	0.67
RIPAR_50 (0.04; 0.02)	101.57	1.16	0.17	0.57	0.45
MAJDRAIN_DIST (-0.00;<0.00) + BUFF_COVER (0.06; 0.02)	102.58	2.16	0.10	8.20	0.41
MAJDRAIN_DIST (<0.00;<0.00) + RIPAR_50 (0.02; 0.01)	103.59	3.17	0.06	10.70	0.22
RIPAR_50 (0.02; 0.01) + TUSACK (<0.00; 0.03)	103.73	3.31	0.06	9.10	0.17
Constant only (null) model	105.94	-	-	-	-

^aModels include the 95% confidence set with models ranked by AIC_c values. Also shown are the criterion values (Δ_i), Akaike's weights (w_i) and the χ^2 , p -values from the Hosmer and Lemeshow goodness-of-fit tests and the AIC_c value of the constant only model. All numbers are rounded to two decimal places. AIC_c , Akaike's Information Criterion; MAJDRAIN_DIST, distance (m) to nearest major drainage line; RIPAR_50, area of riparian woodland/grassland within a 50 m radius; BUFF_COVER, % area of *Cenchrus ciliaris* cover within a 50 m radius; TUSACK_COVER, % area of native soft grass cover.

support as explanations for variation in the response variable relative to other models in the set considered. We assessed the relative strength of models subsequent to the best fitting model by comparing the difference in criterion values of the best ranked model (smallest AIC_c value; AIC_{cmin}) with model i (Δ_i) (Symonds & Moussalli, 2011). The best ranked model has a Δ_i value of 0 and subsequent models are scored as $\Delta_i = AIC_{ci} - AIC_{cmin}$, where AIC_{ci} is the AIC_c value of the model being compared with the best ranked model. Models with Δ_i values less than 2 are considered to be essentially as good as the best model in explaining variation in the response, Δ_i values up to 6 should be considered plausible explanations, Δ_i values between 7 and 10 may be rejected, and Δ_i values greater than 10 should be considered implausible and rejected (Burnham & Anderson, 2002; Symonds & Moussalli, 2011). We also calculated Akaike weights (w_i) for each model, which can be interpreted as the probability of a model being the best model of those considered. We

present the 95% confidence set of models, where the summed w_i equals a minimum of 0.95. To test the overall goodness of fit of each model, we applied the Hosmer and Lemeshow statistic. Significant p -values ($p < 0.05$) from this test are evidence of lack of fit (Quinn & Keough, 2002). AIC_c values, difference in criterion values (Δ_i), Akaike weights and diagnostic measures were calculated manually. All other analyses were run in SPSS (PASW Statistics v.17.0).

RESULTS

Over the 12 month period we encountered 29 *P. australis* on the road transect. Of these individuals; 27 were live and two were road-kills, 17 were males (mean SVL=1042 ±49 mm) and 12 were females (mean SVL=810±34 mm). These individuals do not include animals that were recaptured ($n=2$) and only the original capture locations were included in the habitat analysis.

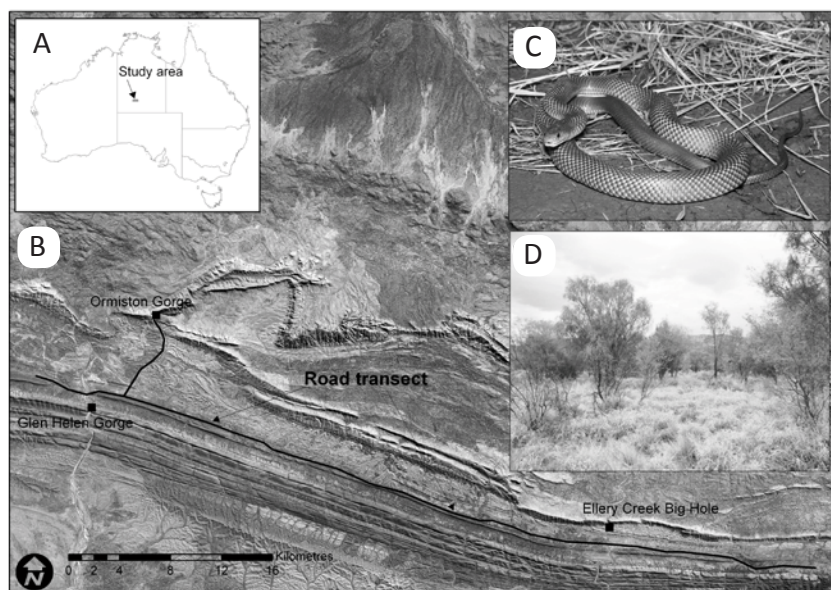


Fig. 1. A) Location of the study area in the Northern Territory, Australia; B) location of the road transect; C) the king brown snake (*Pseudechis australis*); D) typical buffel grass (*Cenchrus ciliaris*) infestation along the road transect, note the dense groundcover.

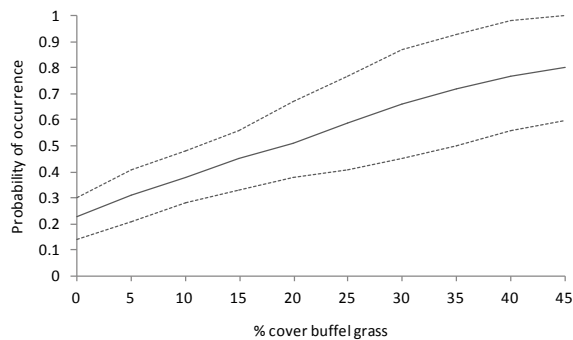


Fig. 2. Relationship between predicted probability of *P. australis* occurrence and % cover of buffel grass within a 50 m radius. Dashed lines represent 95% confidence intervals.

The best AIC_c ranked model included only the variable BUFF_COVER. *Pseudechis australis* were more likely to be located in areas with increased buffel grass cover (Table 2; Fig. 2). This variable was also present in the second and fourth best ranked models. With a total w_i of 0.66 across these three models (1st, 2nd, 4th), together with no evidence of a lack of fit, there is substantial support for BUFF_COVER being a good explanation for variation in the occurrence of *P. australis* (Table 2). There was also some support for RIPAR_50 as an explanation of *P. australis* occurrence. This variable was present in four of the six models within the 95% confidence set, with a combined w_i of 0.54 (Table 2). The other alluvial variable (MAJDRAIN_DIST) was present in two models in the 95% confidence set with a combined w_i of 0.16. *Pseudechis australis* were more likely to be located in closer proximity to major drainage lines, although this relationship was relatively weak (Table 2).

Of the two remaining grass cover variables, HUMCK_COVER was absent from the 95% confidence set and TUSCK_COVER was only present in the lowest ranked model with a w_i of 0.16.

DISCUSSION

The results of the modelling support our hypothesis that *P. australis* exhibit a preference for areas with dense buffel grass. Although there were substantial areas of both spinifex hummock grassland and native tussock grassland along the road transect (McDonald et al., 2012), there was little or no evidence to indicate that either of these grass types influence the occurrence of *P. australis*. This suggests one of two things: i) that *P. australis* prefer dense buffel grass for what it provides (e.g., cover); or ii) that the association with dense buffel grass is an artefact of additional factors not recorded in this study.

In considering the second explanation, because buffel grass tends to occur in areas with run-on hydrology (Miller et al., 2010), it is possible that these areas are more productive than the surrounding landscape and that it is this productivity *per se* that attracts *P. australis*. However, if the association between *P. australis* and buffel grass was related simply to productivity, then it should follow that the riparian woodland and grassland

habitats (the lowest lying and therefore most productive habitat types in all catchments of the study area) would be more strongly related to *P. australis* occurrence than buffel grass itself. Although there was a positive correlation between buffel grass cover and area of riparian habitat within a 50 m radius of sample sites ($r_s=0.51$, $p\leq 0.001$, $n=79$), there were still substantial areas of dense buffel grass in the three other broad habitat types of the study area (chenopod shrublands, acacia shrublands and hummock grasslands; see McDonald et al. 2012), and *P. australis* was regularly encountered in these habitats. This suggests that buffel grass cover itself, rather than productivity, may be the more important factor influencing *P. australis* occurrence.

The establishment and domination of buffel grass invariably results in increased groundcover and this is particularly pronounced in areas that were previously dominated by relatively short-lived native tussock grasses and forbs (Clarke et al., 2005; Miller et al., 2010). As a perennial, the above-ground tussock structure of buffel grass tends to persist longer into low rainfall periods than the annual grasses and forbs (Clarke et al., 2005). In addition, the post-fire response of buffel grass is faster than most native grasses (particularly compared with hummock grasses) and, provided soil moisture is present, can quickly regenerate and return to pre-fire densities (PM, pers. obs.). Together, these factors may result in a preference for buffel grass among those species that are advantaged by dense grass cover, including *P. australis*.

If *P. australis* preferentially select areas of dense buffel grass, then this may be another example of a snake species being ecologically advantaged by an anthropogenic land-cover change. For example, Löwenborg et al. (2010) demonstrated that the grass snake (*Natrix natrix*) has benefited from the presence of manure heaps in rural areas in Europe. Decomposing manure heaps on farms provide the snakes with superior oviposition sites. Higher temperatures, as found within manure heaps, typically resulted in shorter incubation periods, higher hatch success rates, and larger and faster offspring (Löwenborg et al., 2010). This has effectively enabled the grass snakes to penetrate into regions too cold for other oviparous reptile species. Although we are not suggesting that buffel grass has resulted in an overall expansion in the distribution of *P. australis*, it is possible that the presence of this grass has led to an increase in the abundance of the snake in locations where it was formerly uncommon or absent.

Although *P. australis* appears to have benefited from the expansion of buffel grass, other weedy grass species have been shown to have a negative impact. For example, in Wisconsin (USA), Butler's gartersnake was found less frequently in areas dominated by the invasive wetland grass, *Phalaris arundinacea*, probably because the grass has reduced the area of habitat suitable for this rare snake species, although it was unclear why the snake was avoiding *Phalaris* infestations (Kapfer et al., 2013). In Utah (USA), the occurrence of two sympatric snakes was negatively associated with the density of the weed cheatgrass (*Bromus tectorum*), possibly because the grass impeded the mobility of the snakes or dense

infestations supported fewer prey species (Hall et al., 2009).

Investigation of the factors driving the association between *P. australis* and dense buffel grass is beyond the scope of our study and requires further testing (possible hypotheses include increased protection from predators or increased food resources). We also recognize that intraspecific habitat selection in snakes can vary geographically, seasonally and ontogenetically (Reinert, 1993) and that our single study area and relatively small sample size precludes analysis of these factors. However, regardless of what is driving the association, our results have important implications for mitigating the threat to humans and domestic animals posed by *P. australis*. Buffel grass is well established in and around Alice Springs and in many remote Aboriginal communities across the southern NT and northern South Australia. A recognition that *P. australis* may be more likely to be encountered in association with this grass means that efforts to eradicate or reduce the density of buffel grass, particularly in proximity to dwellings, could reduce the risk of interactions between people or domestic animals and this venomous and dangerous elapid.

ACKNOWLEDGEMENTS

This project was partially funded by an operating grant through Charles Sturt University. Dr Chris Pavey and Dr Skye Wassens provided advice on study design and assisted with logistic support. We thank the people who volunteered their time to assist with the snake sampling, including Kelly Knights, Katherine Williams, Gareth Catt, Greg Fyfe, Paul Gardner, Simon Rathbone and Peter Nunn. All snake handling and processing procedures were approved by the Charles Sturt University Animal Care and Ethics Committee (approval number 09/064) and the Department of Natural Resources, Environment, the Arts and Sport/NT Parks and Wildlife Service (research permit number 35656).

REFERENCES

- Albrecht, D.E., Duguid, A.W., Latz, P.K., Coulson, H. & Barritt, M.J. (1997). *Vascular Plant Checklist for the Southern Bioregions of the Northern Territory: Nomenclature, Distribution and Conservation Status*. Alice Springs: Parks and Wildlife Commission of the Northern Territory.
- Brown, W.S. & Parker, W.S. (1976). A ventral scale clipping system for permanently marking snakes (Reptilia, Serpentes). *Journal of Herpetology* 10, 247–249.
- Burnham, K.P. & Anderson, D. (2002). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. 2nd edn. New York: Springer Verlag.
- Burnham, K.P., Anderson, D.R. & Huyvaert, K.P. (2011). AIC model selection and multimodel inference in behavioural ecology: some background, observations, and comparisons. *Behavioural Ecology and Sociobiology* 65, 23–35.
- Clarke, P.J., Latz, P.K. & Albrecht, D.E. (2005). Long-term changes in semi-arid vegetation: Invasion of an exotic perennial grass has larger effects than rainfall variability. *Journal of Vegetation Science* 16, 237–248.
- Currie, B.J. (2004). Snakebite in tropical Australia: a prospective study in the “Top End” of the Northern Territory. *Medical Journal of Australia* 181, 693–698.
- Eyre, T.J., Wang, J., Venz, M.F., Chilcott, C. & Whish, G. (2009). Buffel grass in Queensland’s semi-arid woodlands: response to local and landscape scale variables, and relationship with grass, forb, and reptile richness. *The Rangeland Journal* 31, 293–305.
- Hall, L.K., Mull, J.F. & Cavitt, J.F. (2009). Relationship between cheatgrass coverage and the relative abundance of snakes on Antelope Island, Utah. *Western North American Naturalist* 69, 88–95.
- Kapfer, J.M., Doehler, K. & Hay, R. (2013). The influence of habitat type and the presence of an invasive wetland plant (*Phalaris arundinacea*) on capture rates of sympatric rare and common gartersnake species (*Thamnophis butleri* and *Thamnophis sirtalis*). *Journal of Herpetology* 47, 126–130.
- Löwenborg, K., Shine, R., Kärvelo, S. & Hagman, M. (2010). Grass snakes exploit anthropogenic heat sources to overcome distributional limits imposed by oviparity. *Functional Ecology* 24, 1095–1102.
- McDonald, P.J., Luck, G.W., Pavey, C.R. & Wassens, S. (2012). Importance of fire in influencing the occurrence of snakes in and upland region of arid Australia. *Austral Ecology* 37, 855–864.
- Miller, G., Friedel, M., Adam, P. & Chewings, V. (2010). Ecological impacts of buffel grass (*Cenchrus ciliaris* L.) invasion in central Australia - does field evidence support a fire-invasion feedback? *The Rangeland Journal* 32, 353–365.
- Milne, D.J., Fisher, A., Rainey, I. & Pavey, C.R. (2005). Temporal patterns of bats in the Top End of the Northern Territory, Australia. *Journal of Mammalogy* 86, 909–920.
- Orange, P. (2009). A specialist generalist? Notes on the diet and behaviour of the mulga snake *Pseudechis australis* (Elapidae) in the Kambalda region of Western Australia. *Herpetofauna* 39, 7–13.
- Quinn, G.P. & Keough, M.J. (2002). *Experimental Design and Data Analysis for Biologists*. Cambridge: Cambridge University Press.
- Reinert, H.K. (1993). Habitat selection in snakes. In *Snakes: Ecology and behaviour*, 201–240. Seigel, R.A and Collins J.T. (Eds). New Jersey: The Blackburn Press.
- Rosen, P. C. & Lowe, C. H. (1994). Highway mortality of snakes in the Sonoran Desert of southern Arizona. *Biological Conservation* 68, 143–148
- Shine, R. (1987). The evolution of viviparity: ecological correlates of reproductive mode within a Genus of Australian snakes (*Pseudechis*: Elapidae). *Copeia* 1987, 551–563.
- Smyth, A., Friedel, M. & O’ Malley, C. (2009). The influence of buffel grass (*Cenchrus ciliaris*) on biodiversity in an arid Australian landscape. *The Rangeland Journal* 31, 307–320.
- Symonds, M.R.E. & Moussalli, A. (2011). A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike’s information criterion. *Behavioural Ecology and Sociobiology* 65, 13–21.
- Wilson, S. & Swan, G. (2010). *A complete guide to reptiles of Australia*. Sydney: New Holland Publishers.
- Zuur, A.F., Ieno, E.N. & Elphick, C.S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* 1, 3–14.

Accepted: 14 May 2013