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Is relative abundance a good indicator of population size? Evidence from fragmented populations of a specialist butterfly (Lepidoptera: Lycaenidae).

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Abstract

A common task for conservation biologists and ecologists is to establish how many individuals there are in a population, usually within a defined area of habitat. Estimates of both absolute and relative population sizes are widely used in many aspects of population conservation and management. Mark-recapture studies are appropriate for estimating absolute population sizes of a wide range of animals, both in open and closed populations, while relative abundances can be estimated from a variety of survey methods. Relative abundances are often used in a comparative way to compare both population size and fluctuations in abundance. Here, we used transect counts and capture-recapture studies to estimate the relative abundances and population sizes of a specialist butterfly, *Theclinesthes albocincta* (Lycaenidae) in three habitat fragments, over two consecutive years. The estimates of population size from open and closed mark-recapture models were very similar. The sizes of the three populations differed significantly between sites, and were highly variable between years. One population was extremely small and is likely to become locally extinct. We found that estimates of relative abundance were highly correlated with estimates of absolute population size (r = 0.96, p = 0.009). The combination of transect counts and capture-recapture studies used in this study appears to be a very informative tool for the conservation and management of this butterfly species, and could be extended to other insects.

Keywords: Mark-recapture, transect, population models, monitoring, landscape.

Introduction

Various methods exist to estimate the abundance of populations (Marques et al., 2001; Mattoni et al., 2001; Newman et al., 2003), but generally animal populations can be either surveyed visually (Brown and Boyce, 1998; Royer et al., 1998) using standardised replicated surveys (Mattoni et al., 2001), or by more intensive methods employing mark-recapture techniques (Gall, 1984; Baker, 2004; Chao and Huggins, 2005; Pollack and Alpizar-Jara, 2005). The former approach commonly employs a transect survey that records the number of individuals observed over a set distance through a habitat (Pollard, 1977; Brown and Boyce, 1998; Freilich et al., 2000). These counts are often interpreted as measures of relative abundance, and can be generated for a single species (Mattoni et al., 2001) or communities of species (Caldas and Robbins, 2003; Collier et al., 2006). Variations in the relative abundance of populations may reflect variation in absolute population sizes (Pollard and Greatorex-Davies, 1998), and can also be used to identify temporal and spatial extinction and colonisation events across a landscape. Mark-recapture studies involve capturing and marking individuals within a population, or groups of sub-populations (Maes et al., 2006) and using the recapture rates to estimate population size, based upon a variety of population models (Gall, 1984; Baker, 2004).

While both methods are commonly employed in population studies, choosing the optimal scheme for detection and monitoring (Zonneveld et al., 2003) species is dictated by financial and labour constraints (Garnett et al., 2003). Furthermore, because modern landscapes consist of numerous fragmented and isolated habitat patches, ecologists and conservation biologists often rely on the transect-based method to estimate a measure of relative population size and to monitor fluctuations in abundance (Pollard, 1977; Moss and Pollard, 1993; Mattoni et al., 2001), because it is less time consuming, and hence can be applied across larger scales and multiple populations, giving a broader indication of a species status. For example, transect counts have been used to monitor fluctuations in butterfly populations in the United Kingdom (Moss and Pollard, 1993; Asher et al., 2001) for the past three decades. These data have documented widespread fluctuations in population size of numerous butterfly species (Pollard and Yates, 1993), as well as range contractions throughout the landscape (Leon-Cortes et al., 2000).

In this study we used both transect counts (Pollard walks; (Pollard, 1977) and mark-recapture studies to estimate the relative abundance and population sizes of the specialist butterfly *Theclinesthes albocincta* (Lycaenidae) in a fragmented landscape. Our aims were to (1) use closed and open population mark-recapture models to estimate the sizes of three populations within a fragmented landscape, and (2) examine the relationships between estimates of absolute population size and relative abundance.

Materials and Methods

Study species

The Bitterbush blue, *Theclinesthes albocincta* (Lycaenidae) is a specialist butterfly that is restricted in South Australia to coastal dune habitats (Braby, 2000), where it’s host plant, *Adriana quadripartita* (Euphorbiaceae) occurs

(Gross and Whalen, 1996). Peak flight periods occur from October-April coinciding with the flowering of *A. quadripartita*. Females oviposit on the male inflorescences and the larvae consume the developing pollen within the immature flowers (Grund and Sibatani, 1975). In the Fleurieu Peninsula region of South Australia the range of *Theclinesthes albocincta* has contracted dramatically in historical times, through habitat destruction following the development of coastal zone locations for housing and commercial purposes (Sands and New, 2002). Three fragmented populations of this butterfly occur within the Fleurieu Peninsula region, and these were the focus of our study (Fig. 1).

Capture-recapture experiments and Pollard walk surveys (Pollard, 1977) were conducted at these sites during the Summer of 2004-05 and 2005-06 (Fig. 1). We carried out the surveys and capture-recapture studies during the flowering period of *A. quadripartita*, which occurs for approximately 4-12 weeks during the Spring and Summer months. Pollard walks and mark-recapture studies were performed between 1000h and 1600h in sunny conditions (<40% cloud cover) with minimal wind (<3 Beaufort scale) in order to reduce any possible variation in capture rates and transect counts due to environmental conditions. Before the start of each field day a coin was flipped to decide which task to perform first, either the transect survey or the mark-recapture, to balance any potential impacts (e.g. presence of observer, disturbance) that one task may have had on the other.

Transect counts

Counts of *Theclinesthes albocincta* butterflies were made using Pollard walk surveys (Pollard, 1977) along a single transect that traversed the length of each site. Counts were made on five consecutive days in each of two successive years. All butterflies that flew within 10m of the observer were recorded.

Mark-recapture studies

We conducted capture-recapture studies by searching for *Theclinesthes albocincta* adults for 1.5 hr/d for five consecutive days. During that time the observer walked through the site searching for adult butterflies and captured them with a hand net. The search route through the site roughly followed the Pollard walk transect but the observer was able to deviate laterally to search for and capture as many butterflies as possible. The observer was able to stop walking and backtrack to capture butterflies, unlike the procedure followed on the Pollard walks. Captured butterflies were marked with an individual number on the underside of either of the hind wings using a permanent pen (Staedtler Lumocolor®). The butterfly was then released at the point of capture and searching recommenced. On a few occasions marked butterflies were observed on host plants and their number was readable to the observer. We counted these butterflies as recaptures if the marks on the underside of the wing were readable and unambiguous.

Analyses

We used the SPSS statistical package version 12 (2003) to perform repeated measures ANOVA to test for the effects of site and year on the numbers of observed and captured butterflies. This test was performed to account for the temporal pseudoreplication of the count data, and ultimately to avoid Type I errors (Crawley, 2002). Tukey's post-hoc tests were performed to establish which sites differed significantly from each other in the number of observed and captured butterflies.

We used the software program MARK version 4.2 (White and Burnham, 1999) to calculate estimates of population size of *Theclinesthes albocincta* using the closed population models of Otis et al. (1978). We assumed initially that the populations were closed (i.e. negligible births and deaths) because of the short duration of the studies (Freilich et al., 2000) and the isolation of the populations (i.e. no migration; unpublished data) (Chao, 2001). The closed-capture population models in MARK calculate capture (p) and recapture (c) probabilities of individuals within the population, subsequently allowing the population size, N, to be estimated. We examined three models that allow for three types of variation in p and c. The first model, M_o, does not allow any variation in capture and recapture probabilities. In this model c=p, which are both fixed over time. Secondly, model M_t allows for capture probability (c) to vary by time, and as with the first model, c=p. Thirdly, model M_b allows for variation in capture probability due to behavioural responses to capturing and recapturing animals. When animals are captured and handled they may change their behaviour and become 'trap happy' and are attracted to subsequent trapping events (Hill et al., 2001). Alternatively, animals may become 'trap averse' and avoid encountering another trapping event.

Models (M_o, M_t, M_b) were run using the five day capture-recapture histories of *Theclinesthes albocincta*. No covariates (e.g. sex, age) were included in the models. We chose the model with the lowest Akaike's Information Criterion (AIC) to estimate which model best fit the data (Chao and Huggins, 2005). The AIC is calculated using the formula:

$$\text{AIC} = -2 \ln(L) + 2K$$

where L is the model likelihood, and K is the number of parameters used in the model. Thus, the AIC depends on the model likelihood and the number of parameters included in the model.

We also calculated estimates of population size using Cormack-Jolly-Seber (CJS) open population models (Pollack and Alpizar-Jara, 2005). We wanted to determine whether the assumptions of no migration and no births and deaths were affecting the estimates of absolute population size. We used the 'MRAWIN' version 5 statistical package within R version 2.1.1 (2005) to run four Cormack-Jolly-Seber open population models using the same datasets. The CJS open population models estimate survival (Φ) and capture (p) probabilities that can be either fixed (.) or variable (t) over time (i.e. each variable combination result in a total of four possible models). Again, we used the AIC criteria to decide which model provided the best fit to the data (Pollack and Alpizar-Jara, 2005).

Pearson's correlation was used to test for any significant relationship between the average number of butterflies observed and the estimated population size from the capture recapture surveys.

Results

Pollard walks

Repeated measures ANOVA revealed a significant effect of site on the number of observed ($F_{2,2}$ = 155.611, p = 0.006; Fig. 2a) and captured butterflies ($F_{2,2}$ = 46.169, p = 0.021; Fig. 2b). No significant effect of year was detected on the number of observed ($F_{1,2}$ = 1.614, p = 0.332; Fig. 2a) or captured ($F_{1,2}$ = 1.592, p = 0.334; Fig. 2b) butterflies. Although, the percentage of total recaptured butterflies was higher in year two for Torrens Island (15% and 37% respectively) and Port Gawler (4% and 8% respectively). Tukey's tests indicated that the Port Gawler population was significantly larger than Torrens Island, and Torrens Island was significantly larger than Newland Head (Fig. 2) based on the number of observed butterflies. Furthermore, fewer butterflies were captured at Newland Head compared to Torrens Island and Port Gawler but there was no difference between Torrens Island and Port Gawler (Fig. 2).

Closed population models

Models M_t and M_o best fit the data for Torrens Island and Port Gawler in years one and two respectively (Table 1). There was no result for model M_b for Port Gawler in year two of the study because MARK did not reach the necessary convergence criterion for that particular model. Model M_b best fit the Newland Head 2005-06 data. Population sizes, as predicted from these models, varied considerably between sites and also within sites between successive years (Fig. 4). Port Gawler had the largest estimated population size followed by Torrens Island and Newland Head (Table 1; Fig. 4). Mean population sizes at Torrens Island and Port Gawler were higher in year one compared to years two (Table 1; Fig. 3) and there is considerable variability in these estimates.

The results from both the open (Table 2) and closed (Table 1) population modelling indicated that Port Gawler is the largest of the three *T. albocincta* populations on the Fleurieu Peninsula, followed by Torrens Island and Newland Head (Fig. 4). The Port Gawler and Torrens Island populations showed a decline in population size estimate in the second year of the study. According to the MARK and CJS population size estimates, Torrens Island declined by approximately two thirds in the second year of the study (Fig. 4a) and Port Gawler declined by approximately one third (Fig. 4b).

Open population models

Only two of the four models used were considered to best fit any of the datasets (Table 2). The model assuming variable survivorship through time and a constant capture probability ($\Phi_t p.$) was determined to best fit the Torrens Island in 2004-05 and the Newland Head in 2005-06 datasets based on the lowest AICc scores. The model assuming constant survival and capture probabilities ($\Phi_. p.$) best fit the Torrens Island 2005-06 dataset, and both of the Port Gawler datasets, based on the lowest AIC scores. There are no estimates for Newland Head for the model assuming a constant survivorship and capture probability through time ($\Phi.p.$) because the necessary convergence criterion was not met.

The mean population size estimates derived from the CJS open population models were lower than those of the closed models across all sites and years, with the exception of the Port Gawler year one estimate (Table 2; Fig. 4b). As expected, when a population had a very low proportion of recaptured butterflies the more parameterised models estimated population sizes with enormous variation. However, none of these models were the best fit the data so the high variation did not affect the estimates of population sizes.

Relationship between abundance and population size

Pearson's correlation revealed that the transect counts of butterflies were highly correlated with estimates of absolute population size derived from the closed population models of MARK (r = 0.96, p = 0.009; Fig. 3).

Discussion

We have established that relative abundance estimates from transect surveys are highly correlated with estimates of absolute population size for the butterfly *Theclinesthes albocincta* (Fig. 3), but fluctuations in relative abundance may not reflect changes in absolute populations size between years (Fig. 2 & 4). Given that we have established this strong significant relationship (r = 0.96, p = 0.009; Fig. 3), it may be possible to use relative abundance as a reliable indicator of absolute population size for other populations of *Theclinesthes albocincta*.

Very few studies have sought to establish a relationship between relative abundance and absolute population size in order to make predictions or conclusions about a butterfly species' ecology or conservation status (Thomas, 1983; Braby, 1995; Bergman, 2001; Mattoni et al., 2001). This is somewhat surprising considering the frequency in which measures of relative abundance are used to provide relative estimates of population size (Swengel and Swengel, 1997; Krauss et al., 2004). Pollard (1977) compared the relationship between relative abundance and estimates of absolute population size for one population of the small heath butterfly (*Coenonympha pamphilus*) in Monks Wood, England. He found that, within a single population, transect counts were significantly correlated with estimates of population size (data square-root transformed, $r = 0.548$, $p < 0.001$). However, this study only demonstrated a within-site temporal relationship between relative abundance and population size. Pollard (1977) recognised that multiple sites would need to be surveyed to establish a predictive relationship for *C. pamphilus* by stating 'It remains to be demonstrated that the index of abundance obtained is closely related to population size…'. In the present study, we have shown a highly significant relationship in relative abundance and population sizes from mark-recapture studies using data across three sites and two years for *Theclinesthes albocincta* ($r = 0.96$, $p = 0.009$). Consequently, these results greatly increase our confidence in the application of relative abundance measures to assessing the state of multiple butterfly populations throughout a landscape.

We found significant differences in the abundance of *Theclinesthes albocincta* across the three study sites (Fig. 3). Activity levels of insects can vary spatially and temporally across species. Interactions between population density, climate (Ide, 2002), phenology of hosts, and home range behaviour (Mallet et al., 1987) may contribute to variability in abundance and corresponding capture frequencies. Because relative abundance is often used as a proxy measure of change in population size, the variability in daytime abundance and hence the proportion of animals available to be counted (Link and Sauer, 1998) may have implications for the interpretation of population size trends. Indeed, variation in abundance due to within-site variability in activity and sampling time may lead to biased estimates of both relative abundance estimates from count data and population size estimates derived from mark-recapture studies (Warren and Witter, 2002). In this study we standardised the count data to the period when flight activity is presumed to be at it's maximum (i.e. 1000-1600h), as has been done in the majority of butterfly studies (Steffan-Dewenter and Tscharntke, 2000; Rogo and Odulaja, 2001; Simonson et al., 2001). Nevertheless, we suggest that further study is required to gauge the level of population size change that is associated with apparent changes in relative abundance estimates.

In order to account for differences in habitat size in a study region mark-recapture studies are usually conducted over a set time period to standardise the capture effort. Therefore, we would expect that for a standardised search time, and assuming population sizes are equal, recapture rates would be higher for populations in smaller areas than for populations in larger areas. Our results support this prediction (see Tables 1 & 2) with 15 and 35% recaptures at Torrens Island compared to 4 and 8% recaptures at Port Gawler. We also found the variability in the predicted population sizes decreased markedly in the second year of the study. This effect is most likely due to a doubling of the recapture rate of marked butterflies within these two populations. Both capture and recapture rates are likely to improve over time as the practitioner becomes more skilled at detecting and capturing individuals.

The three populations of *T. albocincta* surveyed for this study are the last to remain within the Fleurieu Peninsula region of South Australia, due mainly to habitat destruction along the coastal zone (Braby, 2000). Genetic analyses of these and other non-fragmented populations indicate they suffer from reduced genetic diversity, probably as a result of their size and isolation (Unpublished data). The present study has shown that the Newland Head population, which happens to exist in a conservation park, is probably nearing extinction (< 25 individuals; Fig. 4). The Port Gawler population is the largest of the three (>1000 individuals; Fig. 4), and is therefore probably the most likely to survive based on current estimates (Primack, 1998)(Tables 1 & 2). Although relatively small, the Torrens Island population is, as the name suggests, located on a small island and access to this site is restricted because of the presence of a power station. This population was found to have several hundred individuals (Fig. 4) and is unlikely to be disturbed in the near future.

This study demonstrates that measures of relative abundance are highly correlated with measures of absolute population size and thus may provide a convenient and rapid method for monitoring population sizes of *Theclinesthes albocincta*. Furthermore, these data could be used to assist the conservation and management of this species. If a similar relationship between relative abundance and population size can be established for other species of butterflies, the relatively simple transect count method could be applied across numerous populations so that species can be managed at the landscape level. Such data are very important for the successful monitoring and management of butterfly populations in remnant habitats and managed reserves.

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Table 1. Model results for three populations of *Theclinesthes albocincta* over two years using the program MARK. Akaike's Information Criterion has been used to select the most appropriate models, which are represented in bold. No models were produced for the Newland Head population in year 1 because there were no recaptures in that year. M_o = fixed capture (*c*) and recapture (*p*) probabilities and c=p, M_t = temporal variation in capture and recapture probabilities and c=p, M_b = temporal variation in recapture probability. AICc = Akaike's Information Criterion, ΔAICc = difference in AICc values between one model and a model with the next highest AICc value. Figure in parentheses represent standard error of mean.

Table 2. Summary table of Cormack-Jolly-Seber open population model results for three populations of *Theclinesthes albocincta* over two years. Akaike's Information Criterion has been used to select the most appropriate models, which are represented in bold. No model results were produced for the Newland Head population in year 1 because there were no recaptures in that year. Φ = Survival probability, p = Capture probability, d.f. = Degrees of freedom. Subscript '*t*' denoted temporal variation of the parameter and subscript '.' denotes a constant parameter. Figures in parentheses represent the standard error of the mean population size estimate of the model. ** Model was unable to reach convergence criterion therefore no results were recorded.

Figure 1. Map of Australia showing the region in which the study was conducted. Expanded inset box shows the state of South Australia with the three study sites indicated by numbers; 1 = Torrens Island, 2 = Port Gawler and 3 = Newland Head, where the fieldwork was conducted. Filled box (■) represents the city of Adelaide.

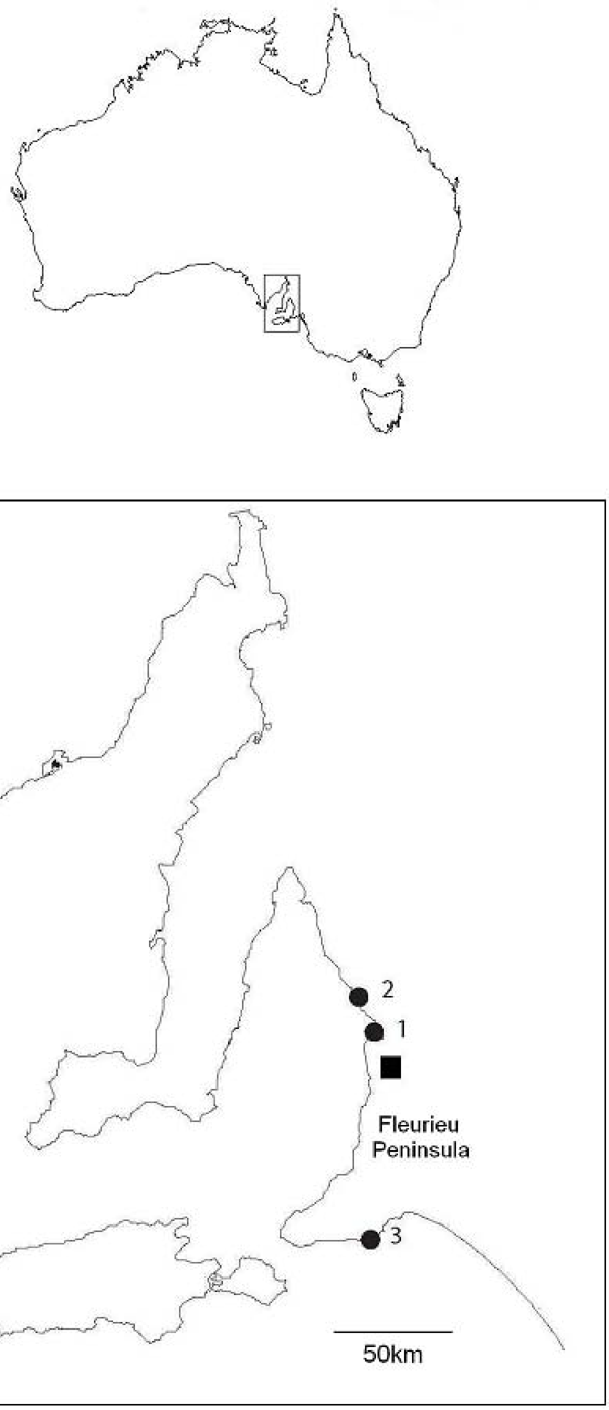
Figure 2. The mean number of (a) observed and (b) captured *Theclinesthes albocincta* butterflies across three sites along the Fleurieu Peninsula over two years (2004-05 (■); 2005-06 (■)). TI = Torrens Island, PG = Port Gawler and NH = Newland Head study sites. Errors bars represent 95% confidence limits of the mean of five consecutive transect surveys.

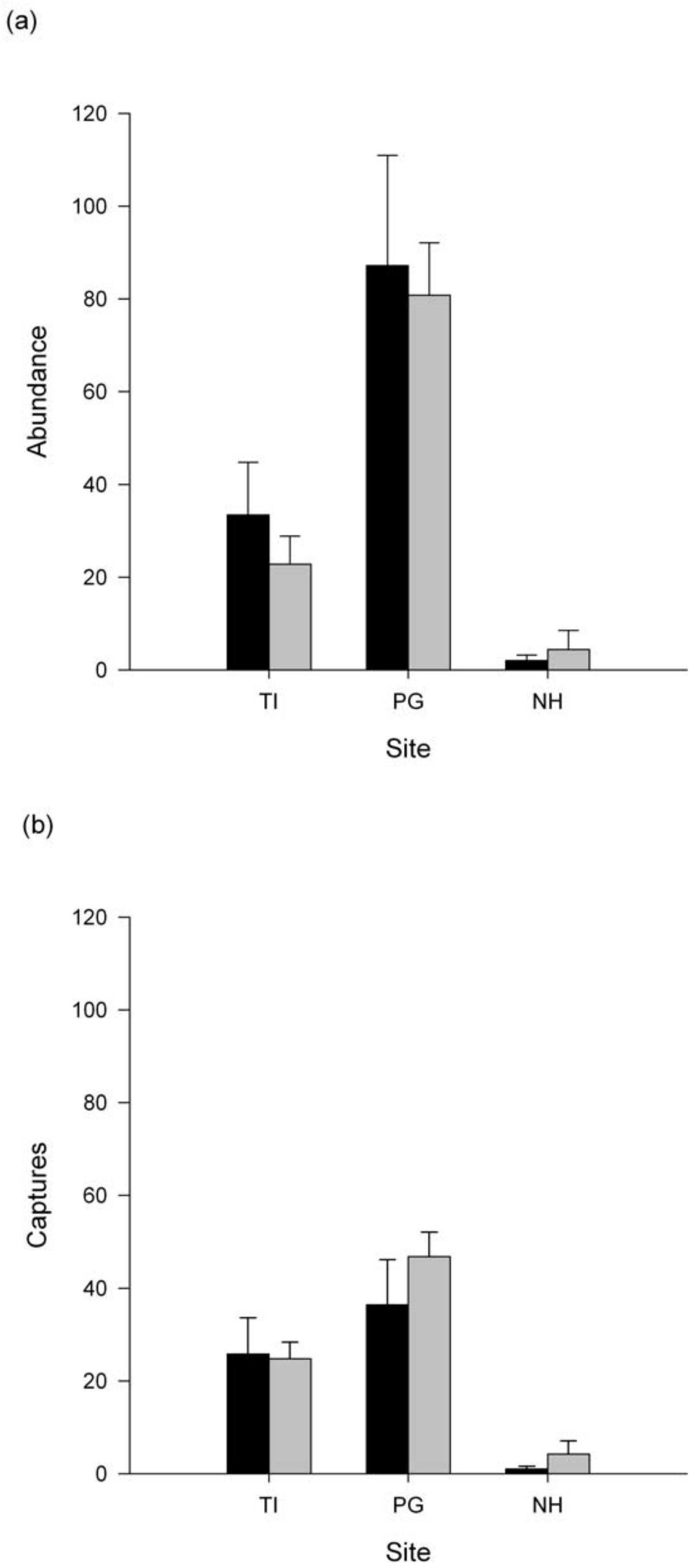
Figure 3. Relationship between the mean number of observed *Theclinesthes albocincta* butterflies and the population size estimates derived from closed population models using MARK. Data points represent the mean of a population size estimate derived from the model that best fit a particular dataset. Data have been pooled within site and year combinations.

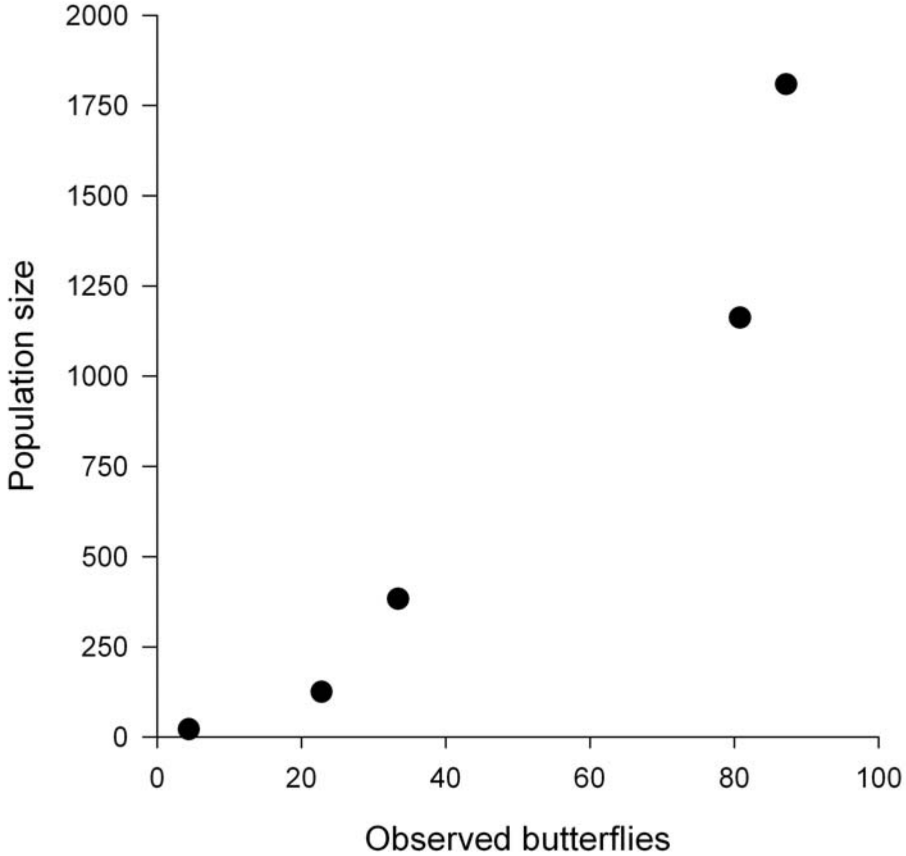
Figure 4. Comparisons of population size estimates of *Theclinesthes albocincta* derived from closed and open population models at three sites along the Fleurieu Peninsula of South Australia (a) Torrens Island, (b) Port Gawler and (c) Newland Head. M1, M2 = population estimates from MARK in 2004-05 and 2005-06 respectively; CJS1, CJS2 = population estimates from Cormack-Jolly-Seber models in 2004-05 and 2005-06 respectively. No estimates of population size (N) were produced for Newland Head (1) because no butterflies were recaptured during mark-recapture studies.

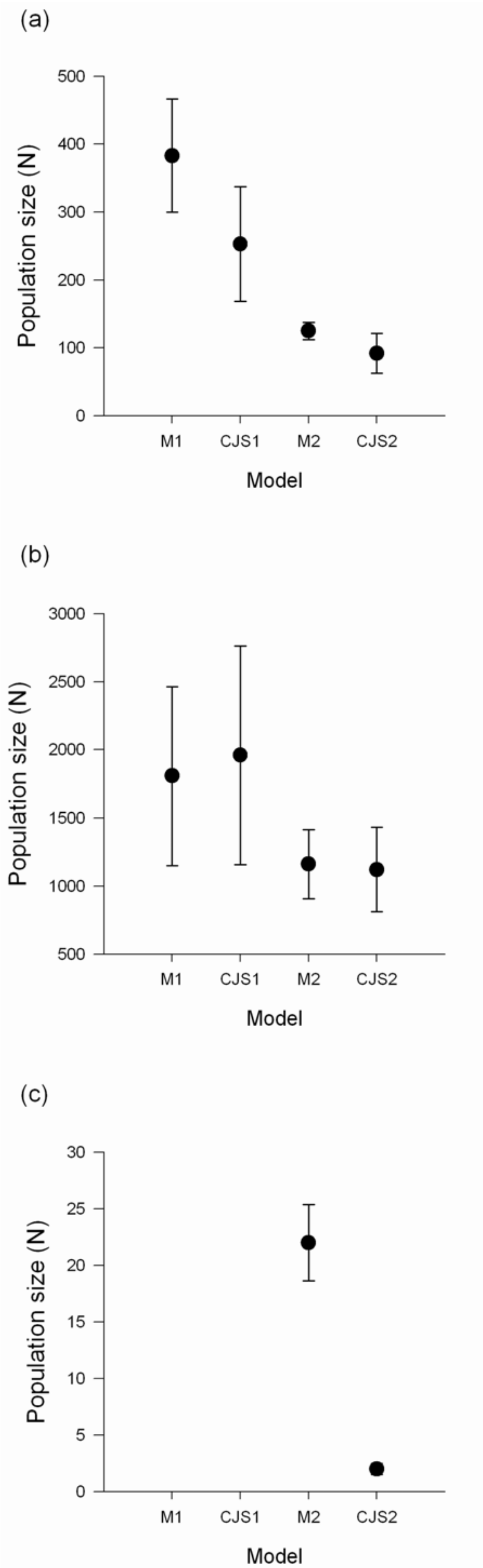
Population	Model	AICc	∆AICc	Model Likelihood	Parameters	Population size (N)
Torrens Island						
Year 1						
	M_o	-364.231	4.26	0.1191	2	
	M_t	**-368.487**	**0**	**1.0000**	**6**	**383 (83.15)**
	M_b	-362.874	5.61	0.0605	3	
Year 2						
	M_o	**-108.929**	**0**	**1.0000**	**2**	**125 (12.72)**
	M_t	-104.204	4.72	0.0942	6	
	M_b	-108.219	0.71	0.7013	3	
Port Gawler						
Year 1						
	M_o	-821.690	4.35	0.1135	2	
	M_t	**-826.042**	**0**	**1.0000**	**6**	**1809 (656.45)**
	M_b	-820.063	5.98	0.0503	3	
Year 2						
	M_o	**-1040.637**	**0**	**1.0000**	**2**	**1162 (252.48)**
	M_t	-1035.721	4.92	0.0856	6	
Newland Head						
Year 2						
	M_o	-2.078	3.44	0.1787	2	
	M_t	-1.918	3.60	0.1649	6	
	M_b	**-5.571**	**0**	**1.0000**	**3**	**22 (3.38)**

Population	Model	AIC	d.f.	Population size (N)
Torrens Island				
Year 1	$\Phi_t p_t$	116.71	7	
	$\Phi.p_t$	120.08	5	
	$\Phi_t p.$	**116.25**	**5**	**253 (84.48)**
	$\Phi.p.$	123.31	2	
Year 2	$\Phi_t p_t$	219.42	8	
	$\Phi.p_t$	213.55	5	
	$\Phi_t p.$	213.66	5	
	$\Phi.p.$	**208.34**	**2**	**92 (29.35)**
Port Gawler				
Year 1	$\Phi_t p_t$	81.36	7	
	$\Phi.p_t$	77.20	4	
	$\Phi_t p.$	77.74	5	
	$\Phi.p.$	**73.25**	**2**	**1961 (803.01)**
Year 2	$\Phi_t p_t$	162.88	8	
	$\Phi.p_t$	157.41	5	
	$\Phi_t p.$	158.48	5	
	$\Phi.p.$	**152.70**	**2**	**1122 (310.63)**
Newland Head				
Year 2	$\Phi_t p_t$	22.50	8	
	$\Phi.p_t$	16.50	5	
	$\Phi_t p.$	**16.50**	**5**	**2 (0.48)**
	$\Phi.p.$**	-	2	


2
1
Fleurieu
Peninsula
3
50km


(a)
120
100
80
60
40
20
0
Abundance
TI
PG
NH
Site
(b)
120
100
80
60
40
20
0
Captures
TI
PG
NH
Site


Population size
2000
1750
1500
1250
1000
750
500
250
0
0
20
40
60
80
100
Observed butterflies


(a)
Population size (N)
500
400
300
200
100
0
M1
CJS1
M2
CJS2
Model
(b)
Population size (N)
3000
2500
2000
1500
1000
500
M1
CJS1
M2
CJS2
Model
(c)
Population size (N)
30
25
20
15
10
5
0
M1
CJS1
M2
CJS2
Model