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Michael P. Scroggie[1], David M. Forsyth[1] and Andrea R. Brumley[2]

[1]Arthur Rylah Institute for Environmental Research
123 Brown Street, Heidelberg, Victoria 3084

[2] Game Victoria, Department of Primary Industries
574 Main Street, Bairnsdale, Victoria 3875

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Arthur Rylah Institute for Environmental Research
Department of Sustainability and Environment
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Department of Sustainability and Environment
PO Box 137
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Front cover photo: Adult male and adult female deer in the wild (David Young).

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Summary

Hog Deer (*Axis porcinus*) are a popular and highly valued game species in Victoria, with licensed hunters permitted to harvest one male and one female during an annual hunting season during the month of April. All harvested deer must be tagged and presented at a checking station within 24 hours of harvest. A variety of morphological and biological data are recorded for each harvested animal during inspection at the checking stations. The objectives of this study were to (i) summarise biological data collected for all Hog Deer inspected at the four mainland checking stations during 1997–2011 (i.e. excluding Sunday Island, which is owned and managed by the Para Park Co-operative Game Reserve Limited), and (ii) provide recommendations for improving the usefulness of future data collection.

A total of 1122 deer were presented at the mainland checking stations (70.4% male; 29.6% female) during 1997–2011, with annual totals ranging from 38 in 1999 to 111 in 2011. There was little evidence that the number or sex ratio of deer harvested annually changed substantially over the course of the study period. The overall percentages of deer harvested on public (52%) and private (48%) land also did not show any discernable trend during the study period. The ages of deer (estimated by molar eruption and tooth wear) ranged from 1 to 12 years for females and males. Although the age structures differed slightly for females and males, there was no evidence that this changed over the study period, although inconsistent recording of ages limited the opportunity for quantitative analyses of these data.

The maximum dressed weights of female and male Hog Deer were 40 kg and 62 kg, respectively. At a given body length, male deer were found to be substantially heavier than females. There was a weak but significant positive relationship between residual body weight (a size-independent index of body condition) and total rainfall in the preceding 12 months for males (but not for females), likely reflecting increased quality and/or quantity of grass and other vegetation (important foods of Hog Deer in Victoria) in higher rainfall years. Larger, heavier females were more likely to be in reproductive condition. There was little evidence that variation in reproductive status of females was attributable to rainfall.

Both sexes were more likely to be harvested during the first few days of each hunting season, but the trend was stronger for males than females. Most deer were harvested around dawn and dusk, particularly on the mainland. There was no evidence that large-antlered males were preferentially harvested earlier in the season on the mainland, suggesting that selection of animals for harvesting was largely opportunistic. Although hunting effort data were not collected, these results likely reflect an interaction between greater hunter effort when the season begins and greater vulnerability of deer to harvesting when the season begins.

The antler lengths of harvested male deer increased with age, body length and residual body weight, but there was no evidence that antler length was influenced by rainfall. Asymmetry of antlers was greater for older males, and also showed a positive relationship with body length, although both of these effects were relatively weak. There was no significant relationship between antler asymmetry and rainfall.

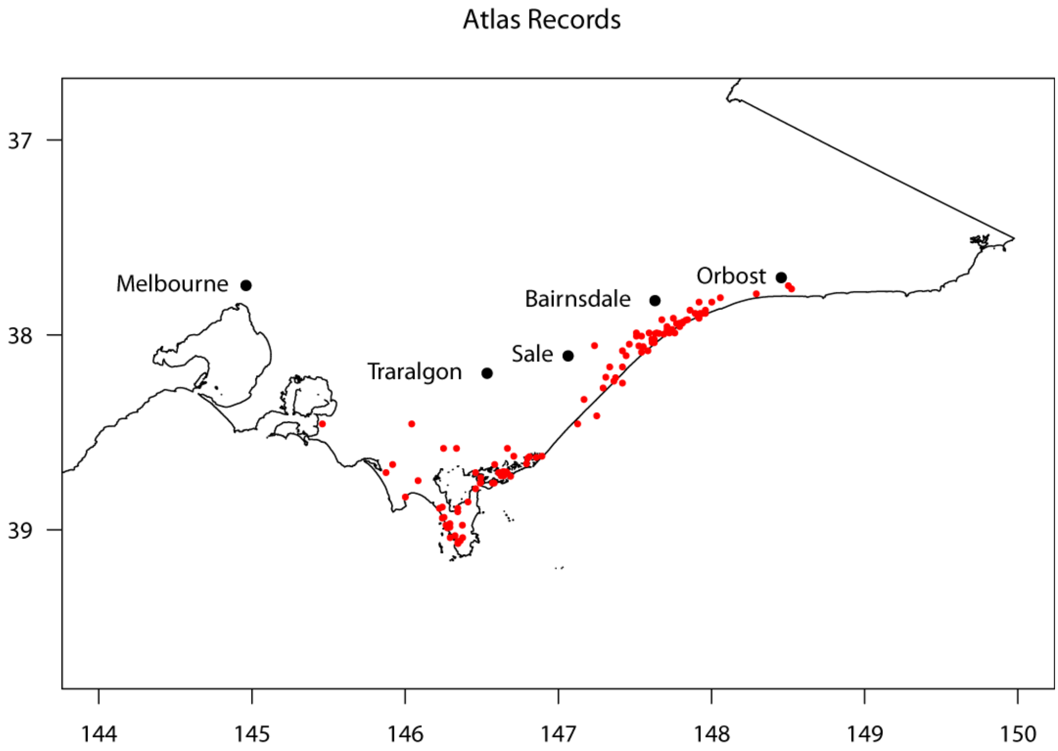
Interpreting trends in the population dynamics of Hog Deer from the harvest data is problematic because changes in harvest may simply reflect changes in hunting effort (which was not measured), rather than any change in the underlying abundance of deer. As total hunting effort was not quantified (i.e. unsuccessful hunting goes unreported), use of catch-per-unit-effort or similar methods to infer trends in abundance from harvest data was not feasible. However, in the absence of hunting effort and population survey information, the relatively constant annual harvest suggests that the size of the Hog Deer population has not changed substantially during 1997–2011. Field surveys assessing the abundance of deer, independent of the harvest data, would be required to determine trends in the abundance of the Victorian Hog Deer population.

We suggest two minor additions to the information currently collected at Hog Deer checking stations. First, that eye lenses are extracted and stored in 95% ethanol for subsequent drying and weighing to provide an alternative and probably more reliable means of estimating ages of older animals. Second, that the weight of the right kidney with and without its associated mesenteric fat be measured so that a kidney fat index (a widely used index of body condition) can be estimated: the kidney fat index is likely to change more rapidly under nutritional stress than the weight/length relationship as environmental conditions vary, and thus may provide a more sensitive indication of the body condition and nutritional status of harvested deer.

1 Introduction

Figure 1. Adult male (left) and adult female Hog Deer on Sunday Island. Note the sexual size dimorphism. (Photo: David Young)

The Hog Deer (*Axis porcinus*; Figure 1) is a small, sexually dimorphic deer (males c. 43 kg, females c. 32 kg; Corbet and Harris 1991) native to the floodplain grasslands and forests of the major Asian river systems, from Vietnam in the east to Pakistan in the west (Mayze and Moore 1990; Dhungel and O'Gara 1991). Two subspecies of Hog Deer are recognised: *Axis porcinus porcinus* (western range) and *Axis porcinus annamiticus* (eastern range). It is *Axis porcinus porcinus* that is most likely to have been introduced into Victoria, having come from India and a translocated population in Sri Lanka (G. Moore, pers. comm.). Hog Deer were released at Corner Inlet, on the eastern Victorian coast, in 1865, and further releases occurred near the Latrobe River at Sale, leading to the establishment of a wild population (Harrison 1998). A captive population was held at Serendip Wildlife Reserve near Geelong and further releases were made at Sale in the 1970s. Captive Hog Deer were released at Blond Bay State Game Reserve in 1984 (D. Young and K. Slee, Australian Deer Association, pers. comm.). The current geographic range of Hog Deer in Victoria includes the coastal strip from just west of Wilsons Promontory in the west, to about Orbost in the east (Figure 2).



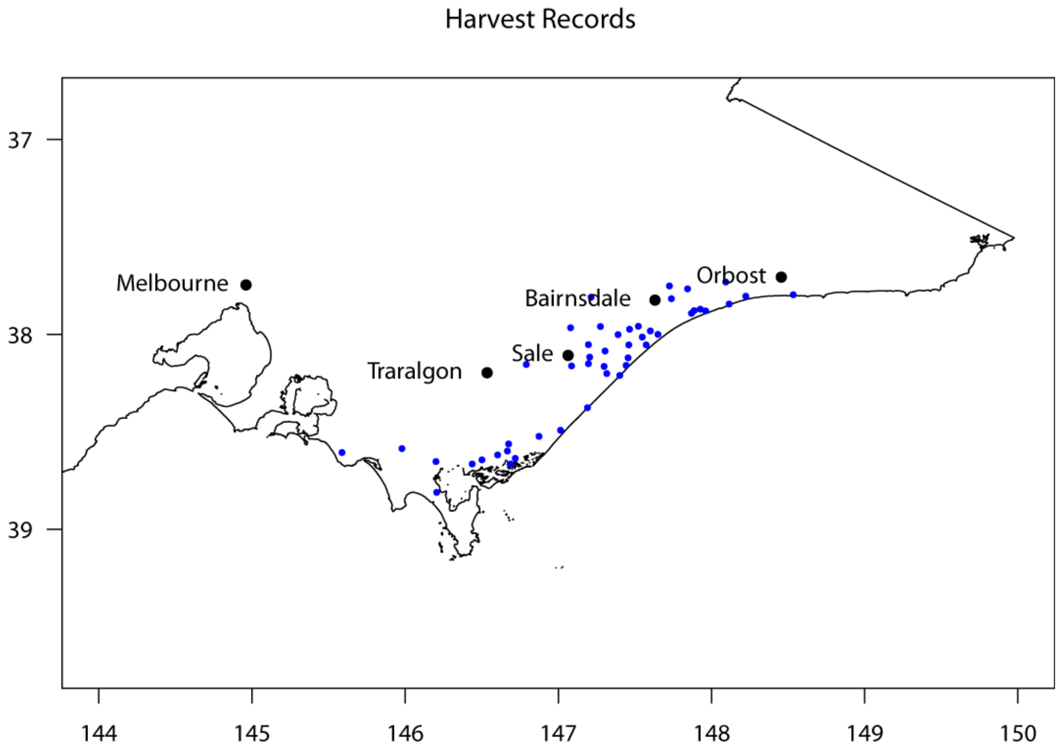


Figure 2. (Top) Locations of Hog Deer recorded in the Atlas of Victorian Wildlife (DSE, 2011). (Bottom) Locations at which hunters reported harvesting Hog Deer on the mainland, between 1997–2011 (54 distinct locations). Scales on the axes of the map denote degrees of longitude and latitude.

Licensed hunters are usually permitted to harvest Hog Deer in Victoria only during the month of April, although on occasion some permits have been provided for limited balloted hunting outside this month. To legally harvest Hog Deer in Victoria, the hunter must hold a Game Licence (‘Deer’) and obtain Hog Deer tags, both issued by the Department of Sustainability and Environment (DSE). A maximum of one male and one female Hog Deer may be harvested by each hunter per season using a centrefire rifle with a calibre of .243 or larger. Bowhunting using compound or long bows of specified draw strengths is also permitted. The Wildlife (Game) Regulations 2001 allow hunting from 30 minutes before sunrise to 30 minutes after sunset. A Hog Deer tag must be attached to the animal by the hunter immediately after harvesting, and the tagged animal must be presented to a checking station for inspection within 24 hours of harvest. Information about the date, time and location of harvest, sex, age, and a variety of body measurements (see below) are recorded for each deer at the checking station, and the data retained by DSE for management and research purposes. This has been a legal requirement since 1997, when checking stations were established.

There have been three or four checking stations on the mainland during 1997–2011, and one on Sunday Island, a 1620-ha island in Corner Inlet that has been managed for the hunting of Hog Deer and other game since it was purchased by the Para Park Co-operative Game Reserve Limited in 1965. Some data concerning total harvest from Sunday Island are also available, along with measurements comparable to those taken from deer harvested on the mainland, facilitating limited comparison of biological and harvest statistics between the mainland and Sunday Island.

Whereas Hog Deer can be legally hunted on any private land during the open season with the permission of the landholder, they can be legally hunted in relatively few areas of public land, all of which are on the mainland. Hog Deer can be legally hunted in six State Game Reserves during the annual open season: Clydebank, Jack Smith Lake, Lake Coleman and Dowd, Ewing and Heart Morasses. In addition to those six reserves, a ballot is held to select hunters to hunt under a special permit in Blond Bay State Game Reserve and part of the Boole Poole Peninsula, the latter in the Gippsland Lakes Coastal Park.

The objective of this study was to use biological data collected at the mainland checking stations during the 1997–2011 Hog Deer hunting seasons to evaluate trends in the following variables: number of animals harvested; percentages of animals harvested on public and private land; sex ratio; female and male age structures; female and male body condition; female reproductive condition; antler length and asymmetry; date and time of the male and female harvests. We also investigated the form of the relationship between shoulder height and body length, and whether body condition and female reproductive condition, and the size and asymmetry of males’ antlers, varied with annual rainfall (which is thought to be an approximate index of food availability).

Finally, we sought to provide recommendations about how the information collected at checking stations could be modified to be more useful for management of Hog Deer. Where appropriate, comparable data collected from Sunday Island have been included in some analyses (see Methods) to increase sample size and to test the generality of patterns observed in data collected on the mainland.

2 Methods

2.1 Data

The following data were recorded for each animal checked at the mainland checking stations: (i) year of harvest (1997–2011), (ii) date of harvest (1–31 April), (iii) time of harvest (24 h clock, frequently rounded to the nearest hour), (iv) sex (male or female), (v) age (estimated from the sequence of molar eruption and tooth wear; Mayze and Moore 1990[1]), (vi) body length (mm; the length from the tip of the nose to the tip of the tail), (vii) girth (mm; the circumference (girth) of the chest), (viii) shoulder height (mm; the distance from the toe to the dorsum of the shoulder), and

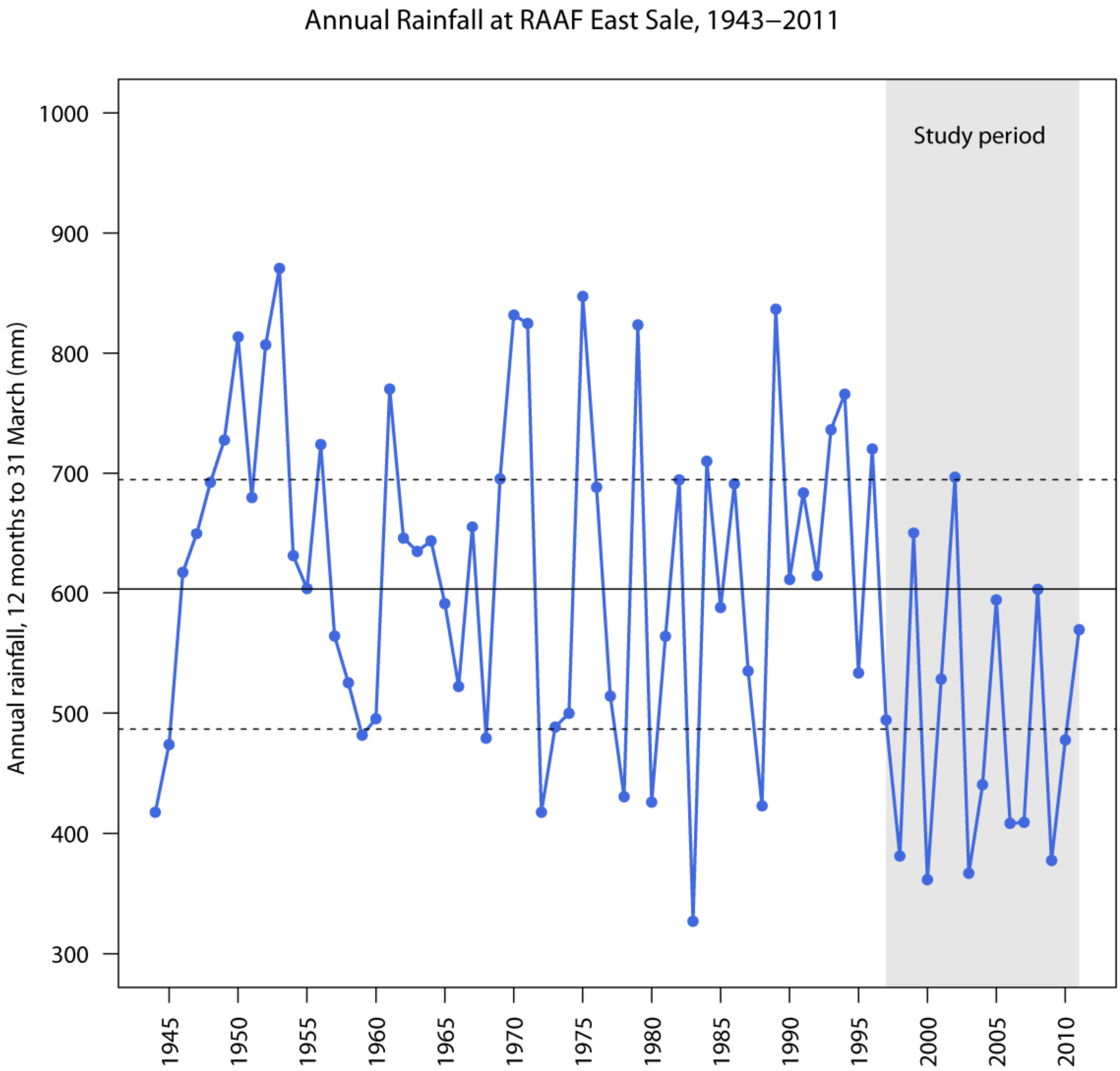


Figure 3. Annual (1 April to 31 March) rainfall recorded at RAAF Base East Sale during 1943–2011. The solid horizontal line denotes the median annual rainfall for this period, and the dashed lines denote the upper and lower quartiles. The period of the current study (1997–2011) is shaded to highlight the lower-than-average rainfall that occurred during most of the study period.

[1] Ages are expressed in completed years from birth, so an animal aged n is in its $n + 1$ year of life (as used for humans).

(ix) body mass (kg; either intact, partially, or fully field-dressed, the latter with the viscera entirely removed). For females the following additional data were recorded: (x) pregnant (whether a foetus was present or not), (xi) lactating (whether there was milk in the teats or not). For males the following additional data were collected: (x) left antler length (mm), (xi) right antler length (mm), (xii) left antler circumference (mm), and (xiii) right antler circumference (mm). The methods used to measure girth, body length and shoulder height are shown in Figure 4.

Figure 4. Geoff Cooper recording body measurements of an adult male Hog Deer at a checking station: girth (upper left), body length (upper right) and shoulder length (lower). Source: Toop (undated). Photo credit: David Needham, DSE.)

We obtained monthly rainfall data for RAAF Base East Sale from the Australian Bureau of Meteorology (www.bom.gov.au). RAAF Base East Sale is close to the centre of the geographic range of Hog Deer in Victoria, so rainfall data for this location were considered to be representative of rainfall in the area subject to harvest. Total rainfall for the 12 months immediately prior to each hunting season were aggregated from the monthly time-series data. These annual totals are reproduced in Figure 3. As pasture growth in south-eastern Australia is often limited by available rainfall, it was considered likely that rainfall would be predictive of food availability and intake for Hog Deer in Gippsland, and thus might be a useful predictor of body condition, antler size, antler asymmetry and reproductive status of harvested deer. This hypothesis was evaluated by constructing statistical models for these biological attributes of individual harvested deer, with rainfall in the 12 months prior to harvest included as a predictor (see 'Data analyses' below).

2.2 Spatial distribution of the Hog Deer harvest

We compared the reported locations at which hunters harvested deer to the known distribution of Hog Deer in Victoria, derived from the Atlas of Victorian Wildlife (DSE 2011).

2.3 Data analyses

For each year of the study period, we collated annual harvest, proportion of harvest on public land, sex ratios of harvested deer, and age structures of harvested deer. These are presented graphically so as to informally evaluate trends in these characteristics of the total harvest. Where available, data for Sunday Island and the mainland are presented separately to allow comparison between harvest statistics for these two locations, which are subject to different management regimes. For some analyses, mainland data from Boole Poole Peninsula was graphed separately. The conduct of balloted hunts at this location meant that differences in the harvest statistics for this location were likely, compared to other mainland harvest sites.

Times of harvest (24 hour clock, rounded to the nearest hour) for deer harvested from both the mainland and Sunday Island are presented as histograms. The temporal distribution of the times of harvest were compared to the times of sunrise and sunset at RAAF Base East Sale on 15 April (i.e. the mid-point of the hunting season) to assess the overall timing of harvests in relation to local sunrise and sunset. To determine if females, males and 'trophy' males (defined as the 25% of males with the longest antlers) were harvested at different times, histograms for each of these subsets of the overall harvest were plotted separately to allow visual comparison of harvest time between these groups. Similarly, times of harvest for Hog Deer from Sunday Island were also plotted separately.

Dates (day of April) that each deer was reported harvested were compiled for the mainland and for Sunday Island. These data were presented as histograms, with the data divided between females, males and trophy males to allow evaluation of the seasonal timing of harvest for these subsets of the population. In particular, the extent to which deer were preferentially harvested near the beginning of the hunting season was evaluated by comparing harvest on the first three days of the season to the remainder of the season. Preferential harvest of trophy males early in the season was also assessed (see analysis of antler length data below).

Linear regression was used to assess the relationship between shoulder height and body length, and body lengths and body masses, of harvested deer. The three variables were log-transformed prior to analysis in order to improve the linearity of the fitted model, and to homogenise the variances of the residuals. Additional factors were included in the regression model to allow for the influence of full or partial field-dressing on measured body masses (field-dressing will reduce the masses of carcasses), and to allow for differences between males and females in the size–weight relationships. The residuals from the overall fitted model were retained, and can be considered to represent an index of body condition for each animal, independent of its body length. Individuals with high residual body weights are thus heavy relative to their body lengths (i.e. can be considered to be in better physical condition).

2.4 Seasonal influences on body condition

As inter-annual variation in pasture biomass in south-eastern Australia is partly regulated by prevailing rainfall (Fitzpatrick and Nix 1970), we hypothesised that in years of higher rainfall there would be more food available to Hog Deer and hence animals would have higher body weights relative to their sizes and ages than in years of lower rainfall. We examined the likely influence of prevailing seasonal conditions (represented by the annual rainfall in the 12 months preceding the hunting season) on body condition by regressing the mean, residual-weight body condition indices (see above) for males and females on annual rainfall to determine if body condition was higher in wetter years.

2.5 Influences on reproductive condition of females

In Victoria, Hog Deer of both sexes probably attain sexual maturity at approximately one year of age, and breeding is not limited to a discrete season although there are probably multiple peak periods (Taylor 1971).

Comprehensive data were available regarding the reproductive status of harvested females for only the mainland (i.e. excluding Sunday Island). Females were considered to be in reproductive condition at the time of harvest if they were either pregnant or were lactating. We used a binomial generalised additive model (Wood 2006) to assess the influence of individual and seasonal factors on the probability of harvested females being in reproductive condition. The model included the potentially non-linear influences of age, body length, residual body weight index (see above) and rainfall during the 12 months preceding the hunting season on the probability of females being in reproductive condition. The generalised additive model provides an assessment of the relative influence of these variables on the probability of females being in reproductive condition.

2.6 Influences on antler length and asymmetry

Data were available regarding the length of each antler for each male Hog Deer harvested on the mainland. Antlers in deer function as sexual ornaments and as weapons used in combat with other males for access to territories and females (Kruuk et al. 2002, 2003; Bartoš and Barbouh 2006).

Although Hog Deer are polygynous, reproductive-aged male Hog Deer in their native range do not appear to hold exclusive territories during the breeding season (Odden and Wegge 2007). Rather, a male will consort with a female in oestrus until mating has occurred (i.e. a ‘tending’ mating system; Weckerly 1998). Fighting between adult male Hog Deer has seldom been observed on Sunday Island despite the high densities of deer there (R. Mayze, pers. comm.), but antlers are easily (and commonly) damaged during the growth stage (Mayze and Moore 1990).

Male Hog Deer with larger antlers are predicted to have higher reproductive success (due to an advantage in combat with other males and through female preferences for larger-antlered mates) than smaller-antlered males. Greater reproductive success amongst males with high levels of symmetry in sexual ornaments such as antlers has also been documented in a wide variety of animal species, including several ungulates (e.g. Bartoš and Barbouh 2006; Ciuti and Apollonio 2011). However, studies of several deer species have not supported that hypothesis (e.g. Kruuk et al. 2003; Pelabon and Joly 2000). Only male Hog Deer grow antlers, which are shed and regrown annually from their second year (Mayze and Moore 1990). Regrowth of antlers has a significant physiological cost, and hence food supply and environmental conditions during the 12 months before the hunting season were considered likely to influence the size and/or symmetry of antlers.

We assessed whether measured biological characteristics of individual males (age, body length and residual body mass) and an environmental variable (annual rainfall prior to the hunting season) influenced the length and asymmetry of antlers using generalised additive models (Wood 2006). For the purposes of the analyses, antler length was defined as the length of the longest antler for each male, while asymmetry was defined as the absolute value of the difference between the lengths of each male’s antlers.

It was suggested to the authors that Hog Deer vary in the degree of antler spread (distance between the tips of the antlers) from east to west across the species' geographic range in Victoria (D. Young and C. Franken, pers. comm.). This hypothesis was evaluated by plotting antler spread for each harvested animal against the approximate longitude of the harvest location. A locally weighted least-squares regression was fitted to the data to assess the form of the underlying relationship between longitude and antler spread.

2.7 Assessment of hunter selectivity for trophy males

Males with large and symmetrical antlers are highly valued by hunters (Mayze and Moore 1990). Males in their first year do not possess antlers, and at two years of age possess two 'spikes'; usually only males aged three years and older grow points (up to a maximum of three on each antler, but occasionally more). We hypothesised that within a single hunting season, hunters may choose to harvest large-antlered males in preference to small-antlered males, due to the higher inherent value placed on these individuals. We assessed this hypothesis by ranking males harvested during each season by antler size, and plotting these ranks against the dates that the males were harvested. If preferential harvest of large-antlered males is occurring, then it would be expected that there would be a preponderance of large-antlered males taken early in the season, with hunters becoming gradually less selective as the available time for legal hunting is depleted, and the availability of preferred, large-antlered males is diminished by harvesting. We tested this hypothesis statistically, by computing the significance of the Spearman rank correlation between antler length and day of harvest, for each year's harvest data.

3 Results

3.1 Spatial distribution of the harvest

The spatial distribution of harvested Hog Deer accords closely with the known distribution of this species in Victoria (Figure 2). Both sets of locational data show the distribution of the species being confined to coastal Gippsland, with very few records (either Atlas or harvest) east of about Orbost or west of Wilsons Promontory.

3.2 Trends in the total annual harvest

The annual reported harvest of Hog Deer on the mainland during 1997–2011 ranged between 38 in 1999 and 111 in 2011 (Figure 5). Harvest data from Sunday Island were only available for 1997–2007, and the annual harvest there ranged from 35 in 2001 to 108 in 2007. The numbers of Hog Deer harvested annually has increased on the mainland and on Sunday Island since 1999–2001.

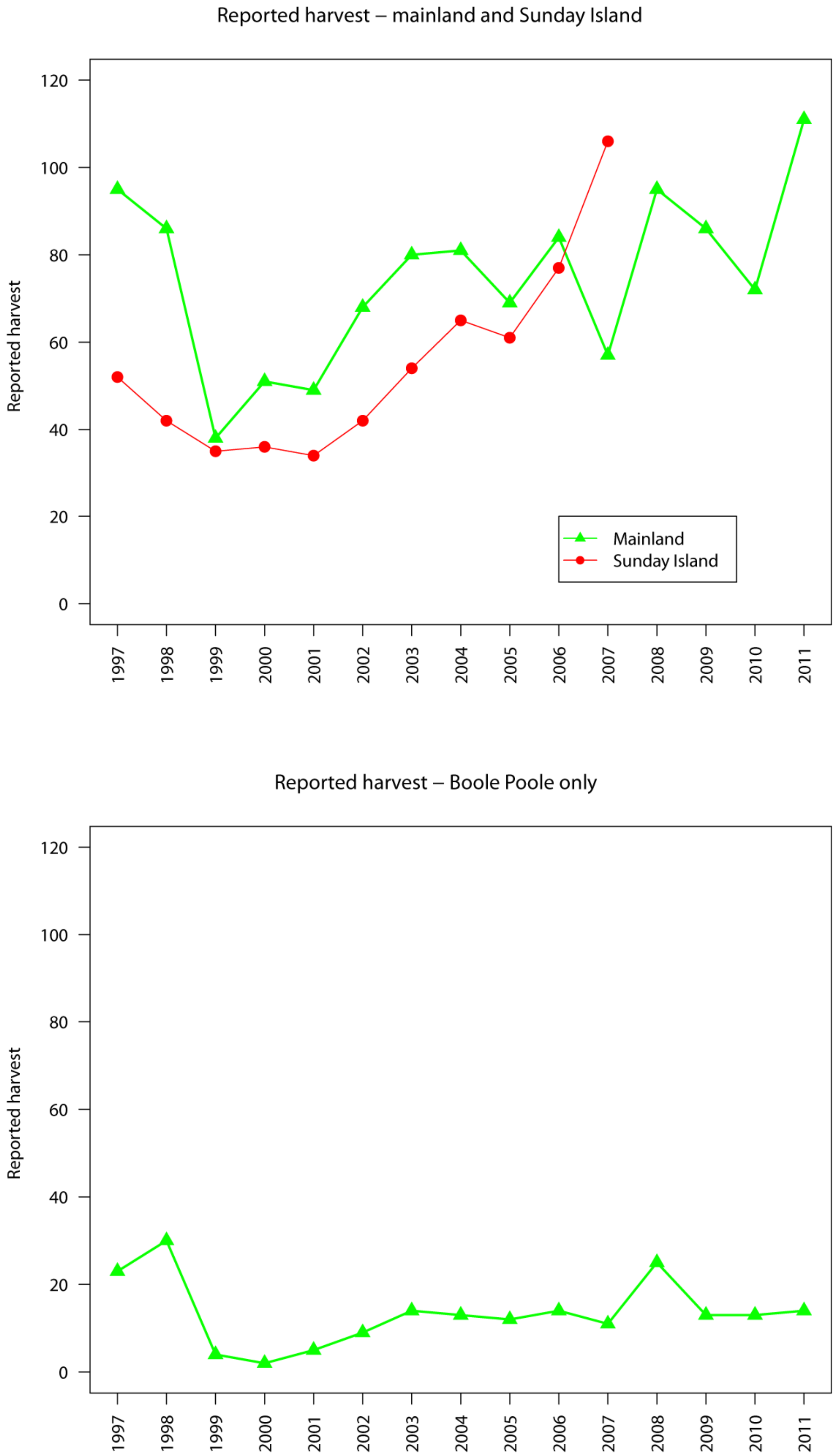


Figure 5. (Top) Annual harvests of Hog Deer from the mainland (n = 1122; 1997–2011) and Sunday Island (n = 604; 1997–2007). (Bottom) Annual harvest for the subset of mainland animals from Boole Poole, an important harvesting location where balloted hunts are conducted.

3.3 Proportion of the mainland harvest on private and public land

Approximately equal proportions of deer were harvested on private and public land on the mainland during each year of the study (Figure 6). The overall percentages of deer harvested on public (52%) and private (48%) land also did not show any noticeable trend during the study period. Note that Sunday Island is private land, and data from there were not included in these analyses.

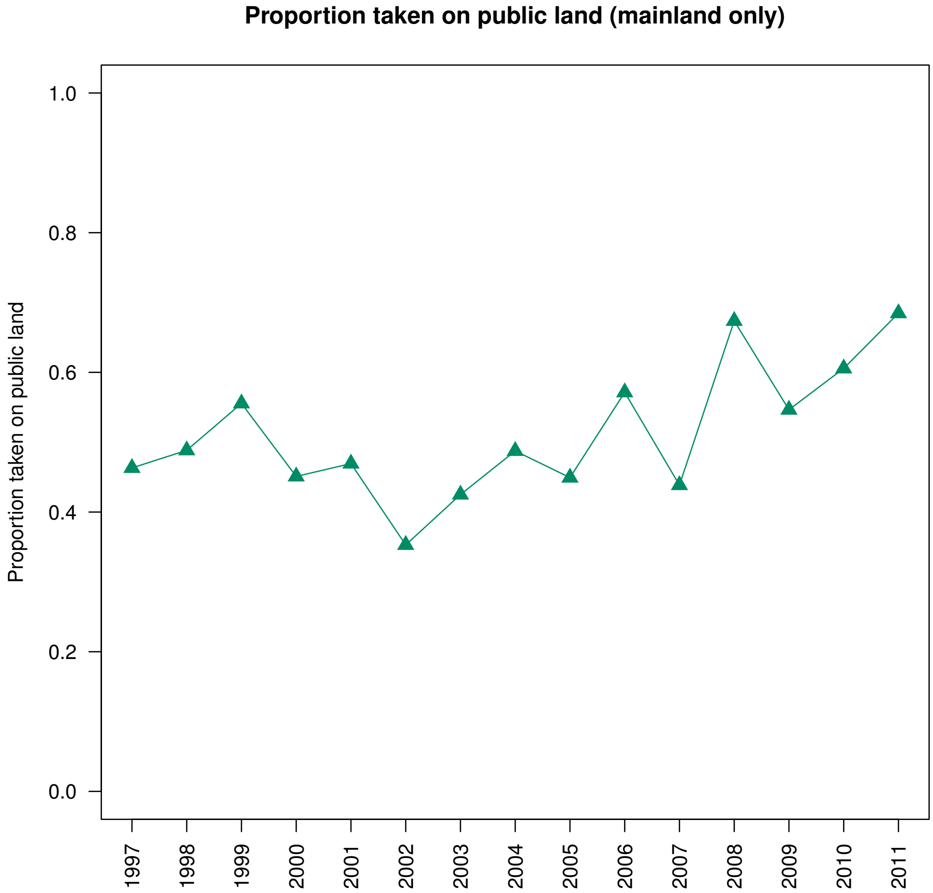
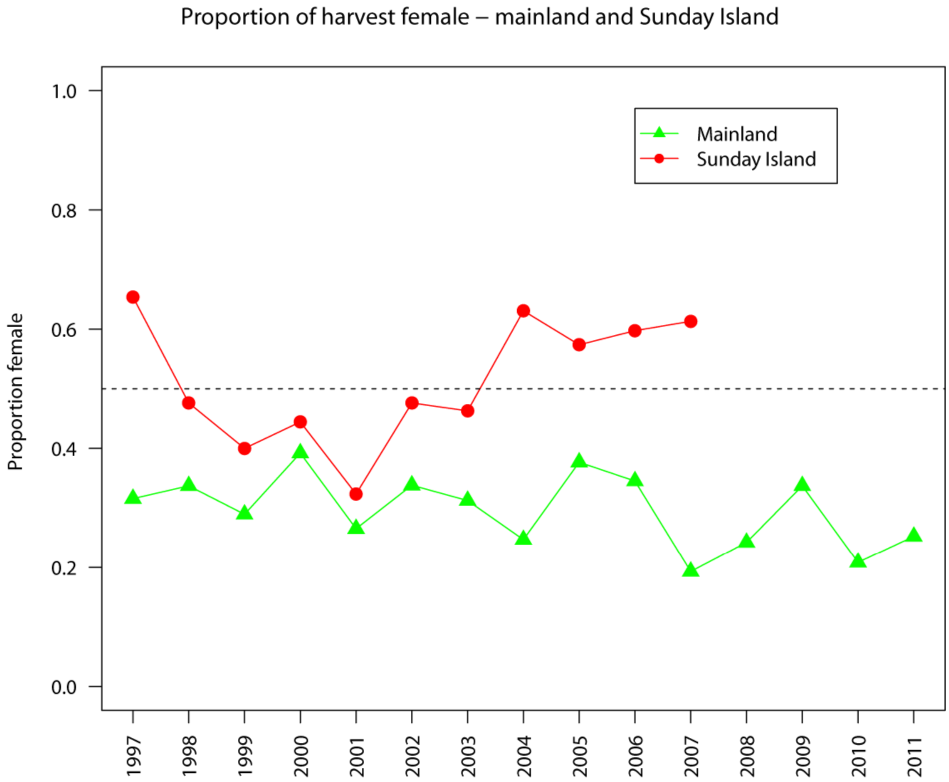


Figure 6. Proportions of Hog Deer (n = 1122) harvested on public (c.f. private) land on the mainland (i.e. excluding Sunday Island) during 1997–2011.

3.4 Sex ratio

Throughout the study period the sex ratio of the mainland harvest was strongly male-biased: in most years approximately 70% of harvested deer were male (Figure 7). This biased sex ratio in the mainland harvest could be a reflection of hunter preference for males but, without information on the underlying sex ratio of the population available to be harvested, formal assessment of this hypothesis is not possible. In a wild Hog Deer populations in India the ratio of females based on counts and observations ranged between 53% (Spillett 1966) and 56% to 85% (Tak and Lamba 1981). On Sunday Island, the sex ratio of harvested deer was much closer to parity in some years, but also subject to large fluctuations, possibly reflecting efforts by the managers (Para Park Co-operative Game Reserve Limited) to manipulate the sex ratio of the Hog Deer population by targeting either males or females for harvest in some years (Figure 7). For animals harvested at Boole Poole, there was a much more strongly male-biased sex ratio in most years than was the case for other mainland locations (Figure 7).



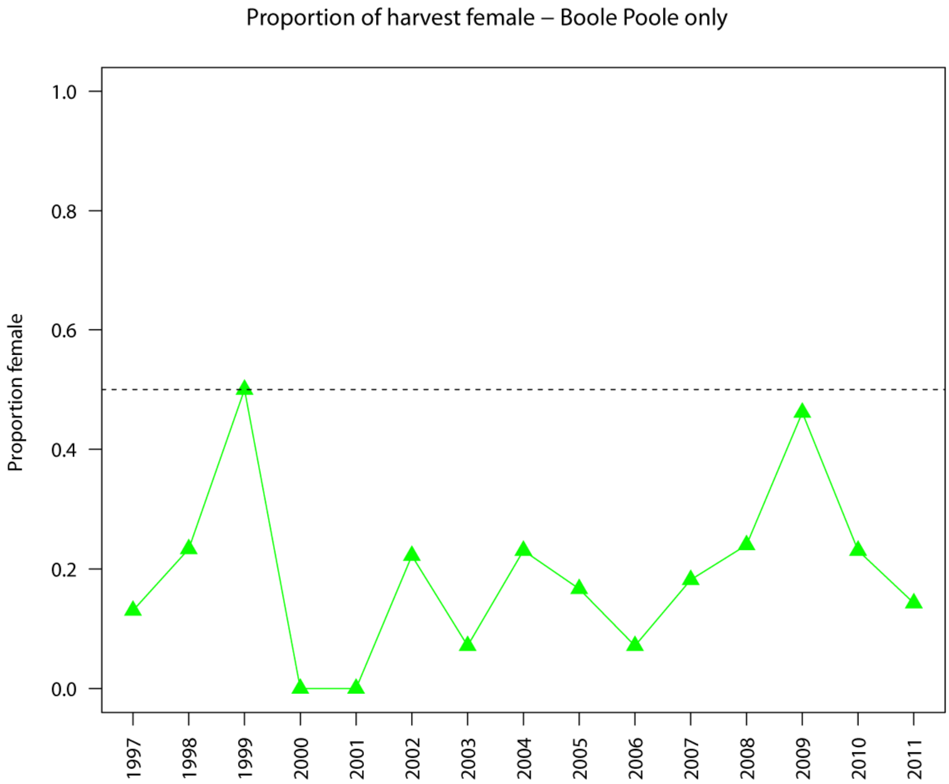


Figure 7. (Top) Proportion of females in the annual harvests of Hog Deer from the mainland (n = 1122) and Sunday Island (n = 604), 1997–2011. (Bottom) Proportion of females in annual harvest from Boole Poole only. The horizontal dashed line is the expected result if equal proportions of male and female deer were harvested.

3.5 Age structure

The estimated ages of harvested deer ranged from 1 to 12 years (Figure 8). In most years, it seems that estimated ages supplied by the checking station operators were truncated at 5+ years, meaning that older animals have not consistently had their ages estimated. In any case, assignment of harvested deer to older age categories can be unreliable because beyond the first few years of life, the pattern of tooth eruption and wear is more variable and less consistent amongst deer of a given age (Hamlin et al. 2000). The reliability of age estimates requires further assessment, and exploration of alternative age-estimation methods, such as eye-lens weights, should be considered (see Discussion). Overall, there was no evidence of gross differences in the age structure of harvested males and females, and the age structure of the Sunday Island harvest seems broadly similar to that of the mainland harvest (Figure 8).

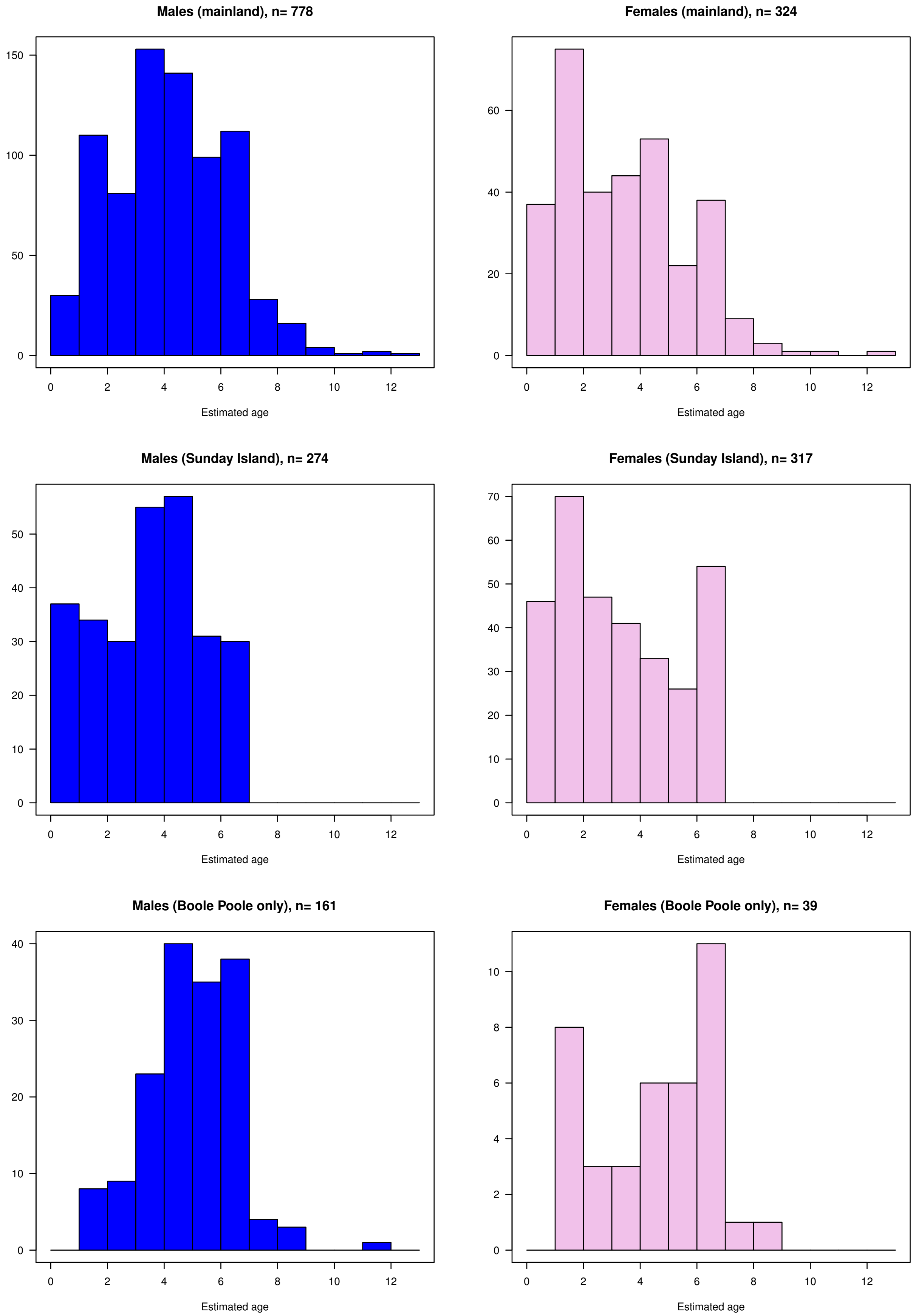


Figure 8. Distribution of estimated ages for females and males harvested from all mainland locations, from Sunday Island and the subset of mainland animals harvested from Boole Poole, 1997–2011.

3.6 Time of harvest

On the mainland, times of harvest were concentrated in the hours immediately before and after sunrise and sunset, with no apparent differentiation in the times that females, males and trophy males were harvested (Figure 9). On Sunday Island, a somewhat different pattern of diurnal variation in hunting success was apparent for both sexes. Harvesting of females was spread more evenly throughout the day whereas males were most commonly harvested at dusk, with a smaller proportion of males taken around dawn than was the case on the mainland (Figure 9). A few deer were reported as having been harvested at times that would not have been consistent with the requirement of the hunting regulations (i.e. the hours of darkness): whether this reflects actual non-compliance, data entry errors, or inadvertant recording of times of attendance at the checking station, rather than times of harvest, is unknown.

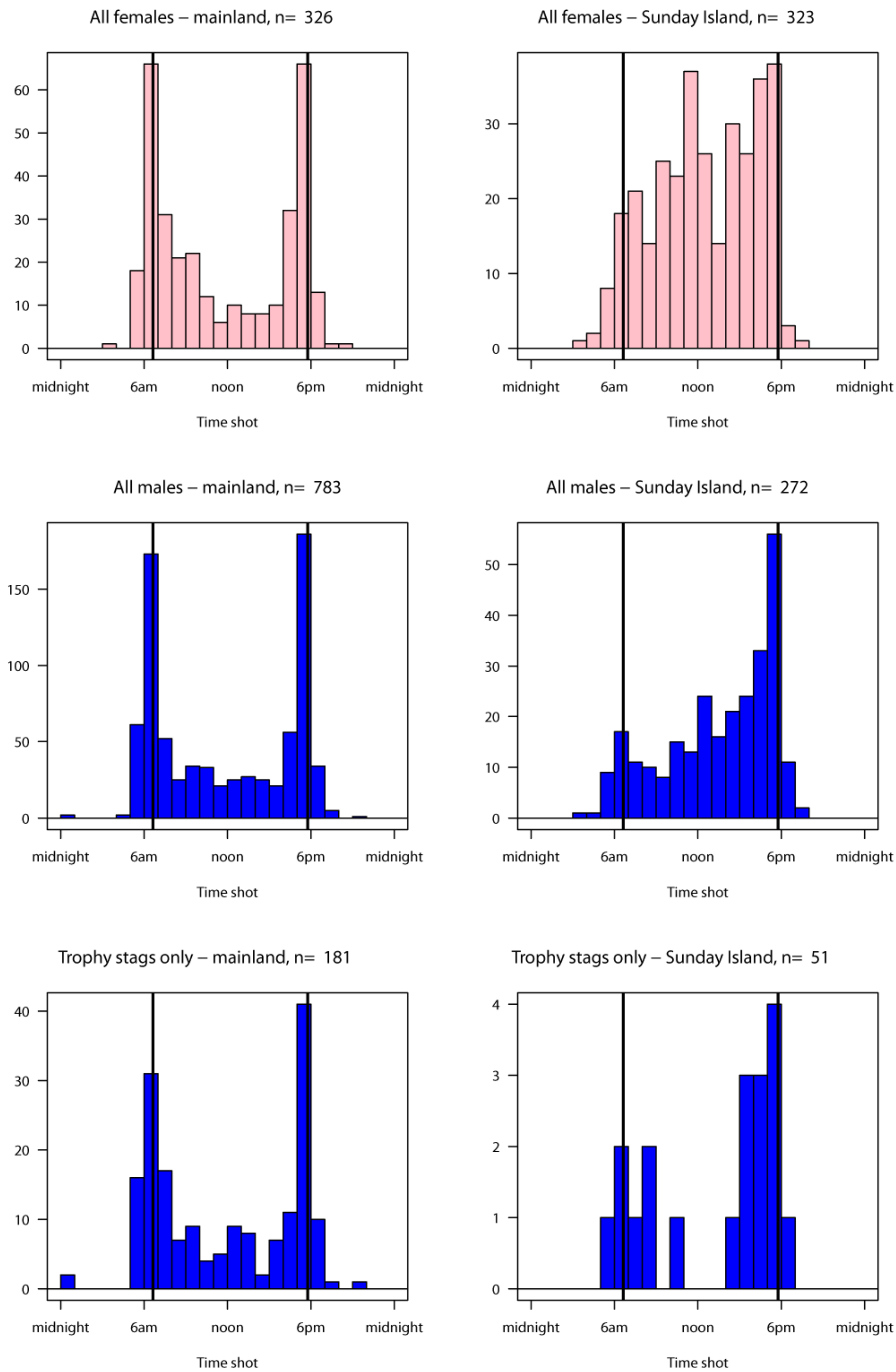


Figure 9. Histograms of times (rounded to nearest hour) that Hog Deer were reported harvested on the mainland (left column) and Sunday Island (right column), during 1997–2011. Deer were divided into three categories: females, males, and trophy males (defined as males with the longest 25% of antlers i.e. > 33cm). The superimposed vertical lines denote the times of sunrise and sunset at RAAF Base East Sale on 15 April, the mid-point of the hunting season. Note that some deer were reportedly harvested at illegal times.

3.7 Harvest date

Hog Deer were harvested throughout the hunting season on the mainland, but the largest daily harvests occurred during the first three days of each season (Figure 10). After about the first seven days of the hunting season, the harvest rate remained approximately constant for the remainder of the season. In contrast to the mainland, harvesting of Hog Deer on Sunday Island was concentrated near the beginning and end of the hunting season for both sexes (Figure 10).

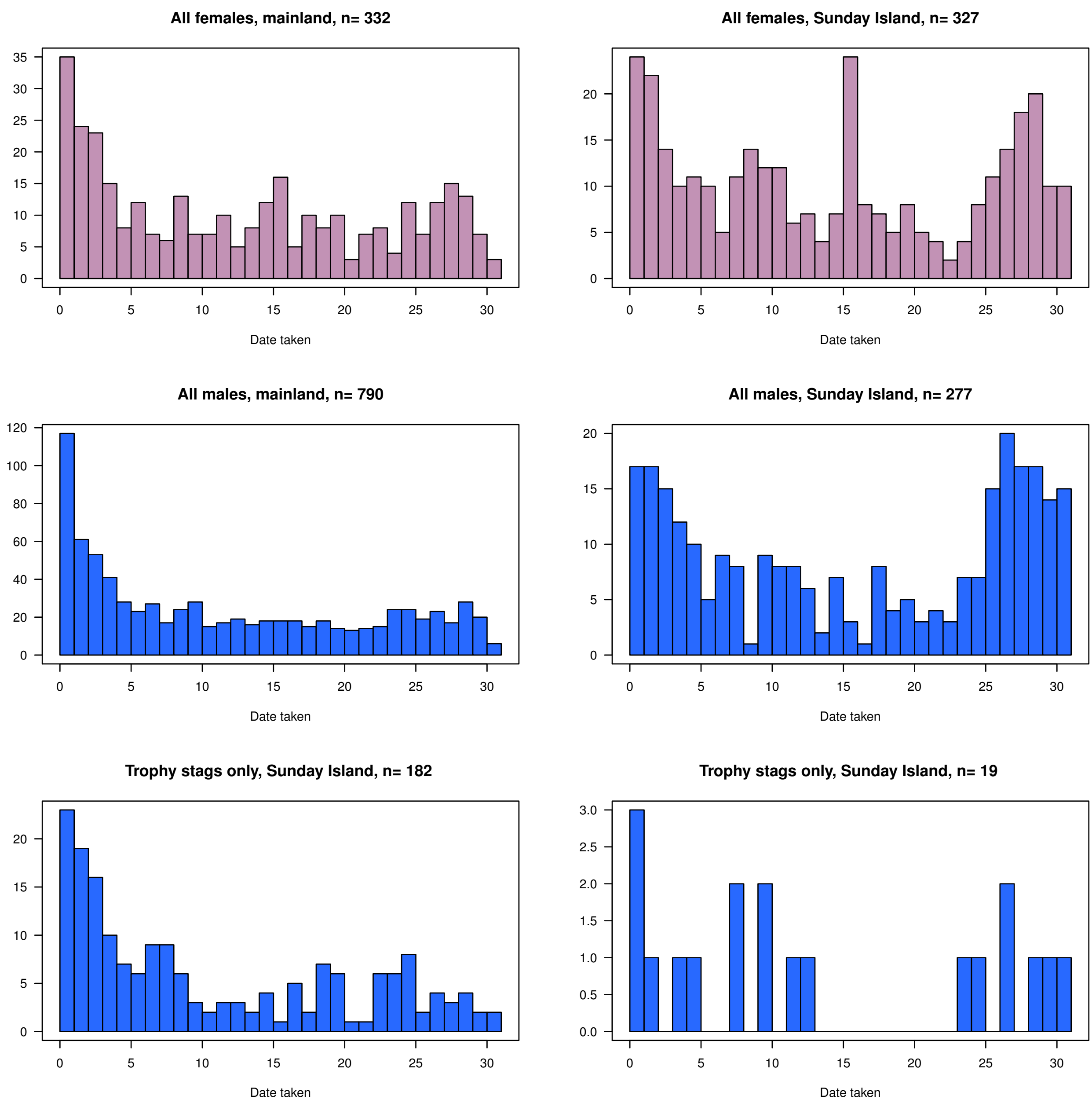
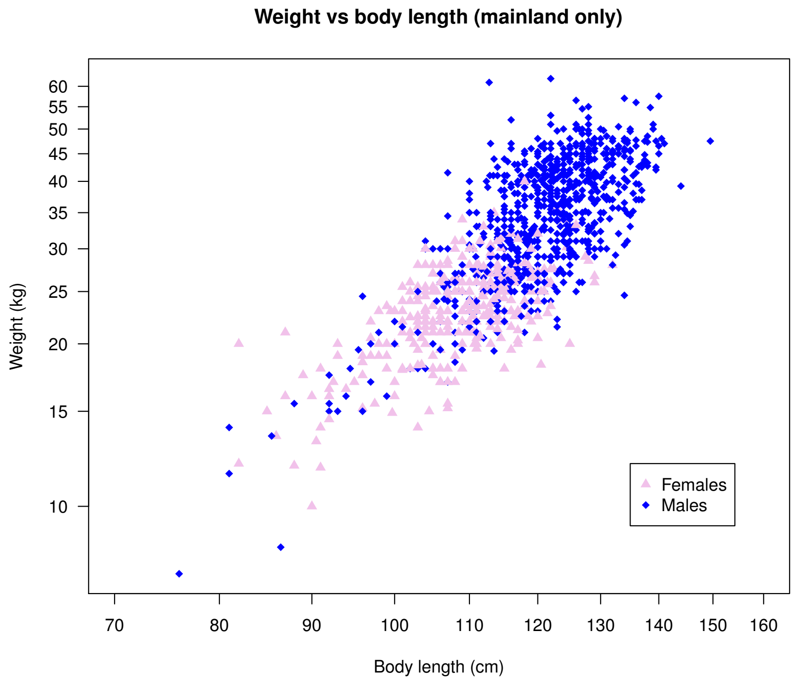


Figure 10. Dates (during April) that female, male and trophy male (defined as the 25% with the longest antlers) Hog Deer were harvested on the mainland and on Sunday Island during 1997–2011.

3.8 Body condition

The maximum dressed weights of a female and male Hog Deer were 40 kg (a 8.5 yr old animal harvested in 2011) and 62 kg (a 3.5 yr old animal harvested in 2007), respectively. Regression analysis showed that body lengths of harvested Hog Deer were a strong predictor of body mass (Figure 11, Table 1). After accounting for the influence of body length on reported weights, it was found that at a given body length, males were heavier than females. The analysis also accounted for the effect of field-dressing on the reported weights of deer: as expected, full and partial field-dressing both led to reductions in reported weights. The residuals of the body length versus mass regression were retained as a size-independent measure of the body condition of individual deer, adjusting for overall body size and the effects of field-dressing and sex. The regression model explained 67% of the observed variation in body weights.



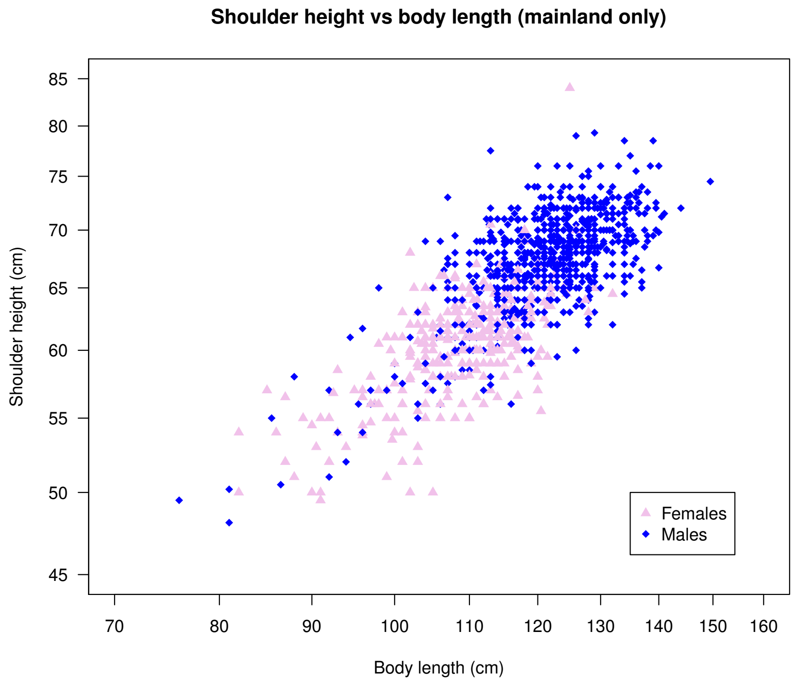


Figure 11. (Top) Relationship between body length (cm) and weight (kg) of female and male Hog Deer harvested on the mainland during 1997–2011. (Bottom) Relationship between body length (cm) and shoulder height (cm) of female and male Hog Deer harvested on the mainland during 1997–2011. Note that the scales of the x and y axes for both panels are logarithmic to improve the linearity of the relationships.

Table 1. Parameter estimates from the linear model of the relationship between body length and body weight for Hog Deer harvested on the mainland and Sunday Island (n = 1104). SE, standard error. The adjusted r^2 for the model was 0.6721.

Parameter	Estimate	SE	t-value	P-value
Intercept	-4.129	0.581	-7.107	<0.0001
Log(body length)	1.630	0.123	13.239	<0.0001
Sex[1]	-3.509	0.694	-5.054	<0.0001
Partly field-dressed[2]	-0.123	0.189	-0.654	0.50
Fully field-dressed[2]	-0.376	0.067	-5.603	<0.0001
Log(body length) × Sex	0.777	0.147	5.283	<0.0001

[1]The reference level for this factor is female.

[2]The reference level for these factors is 'not field dressed'.

3.9 Shoulder height and body length

The maximum shoulder heights for female and male Hog Deer harvested on the mainland were 84 cm (a 4.5 yr old harvested in 2010), and 99.5 cm (a 4.5 yr old harvested in 2011), respectively. The maximum body lengths of female and male Hog Deer were 132 cm (a 4.5 yr old harvested in 2000), and 149 cm (a 4.5 yr old harvested in 2004), respectively. The relationships between body length and shoulder height for male and female Hog Deer harvested on the mainland are presented in Figure 11.

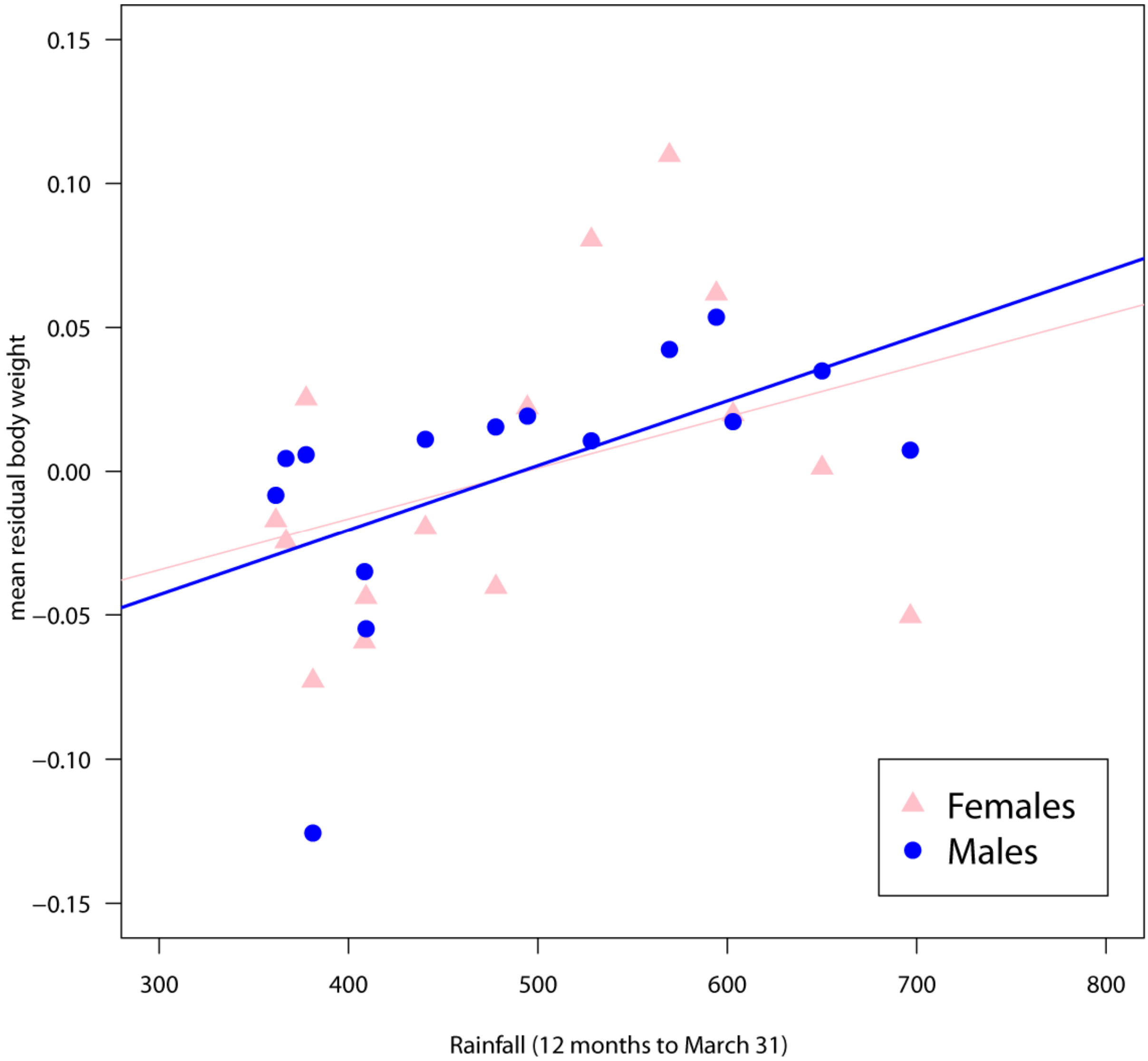


Figure 12. Relationship between residual body weight (derived from the regression of body weight on body length) and rainfall for males and females harvested on the mainland 1997–2011. Deer with large residual body weights are statistically heavy for their sizes. The regression model for males was statistically significant ($p=0.03$, $r^2=0.267$), while that for females was not ($p=0.178$, $r^2=0.068$).

3.10 Reproductive status of females

The proportion of harvested females pregnant each year varied from < 30 % in 2002, to nearly 70 % in several years throughout the study (Figure 13). We analysed individual and seasonal influences on the reproductive states of harvested females using a generalised additive model. The analysis showed that body length and residual body weight were significant predictors of females being in reproductive condition (i.e. either pregnant or lactating) when harvested (Table 2, Figure 14). Females with body lengths <110 cm were much less likely to be reproductive than longer females (Figure 14), and females with high residual body weights were much more likely to be pregnant or lactating at a given size than females with high residual body weights. Estimated age was a weak predictor of female reproductive status after accounting for the influences of body length and weight, and the direction of the effect was unexpected: older females were less likely to be pregnant than younger females after effects of size and weight were accounted for (Figure 14). There was no evidence that female reproductive status varied with rainfall (Figure 14). Much lower proportions of females were reported pregnant or lactating on Sunday Island compared to the mainland, and it is unclear whether this was a real effect or due to data not being collected in a comparable manner. Because the latter possibility could not be ruled out, we did not include data from Sunday Island in our analyses of female reproductive status.

Table 2. Summary of the smoothing terms included in the binomial generalised additive model of the reproductive status of female Hog Deer harvested on the mainland (n = 307). The adjusted r^2 for the model was 0.174.

Parameter	df[1]	Chi-square	P-value
Age	1.000	3.251	0.07
Rainfall	1.649	3.582	0.15
Residual body weight	1.000	11.082	<0.0001
Body length	1.948	24.530	<0.0001

[1]Effective degrees of freedom.

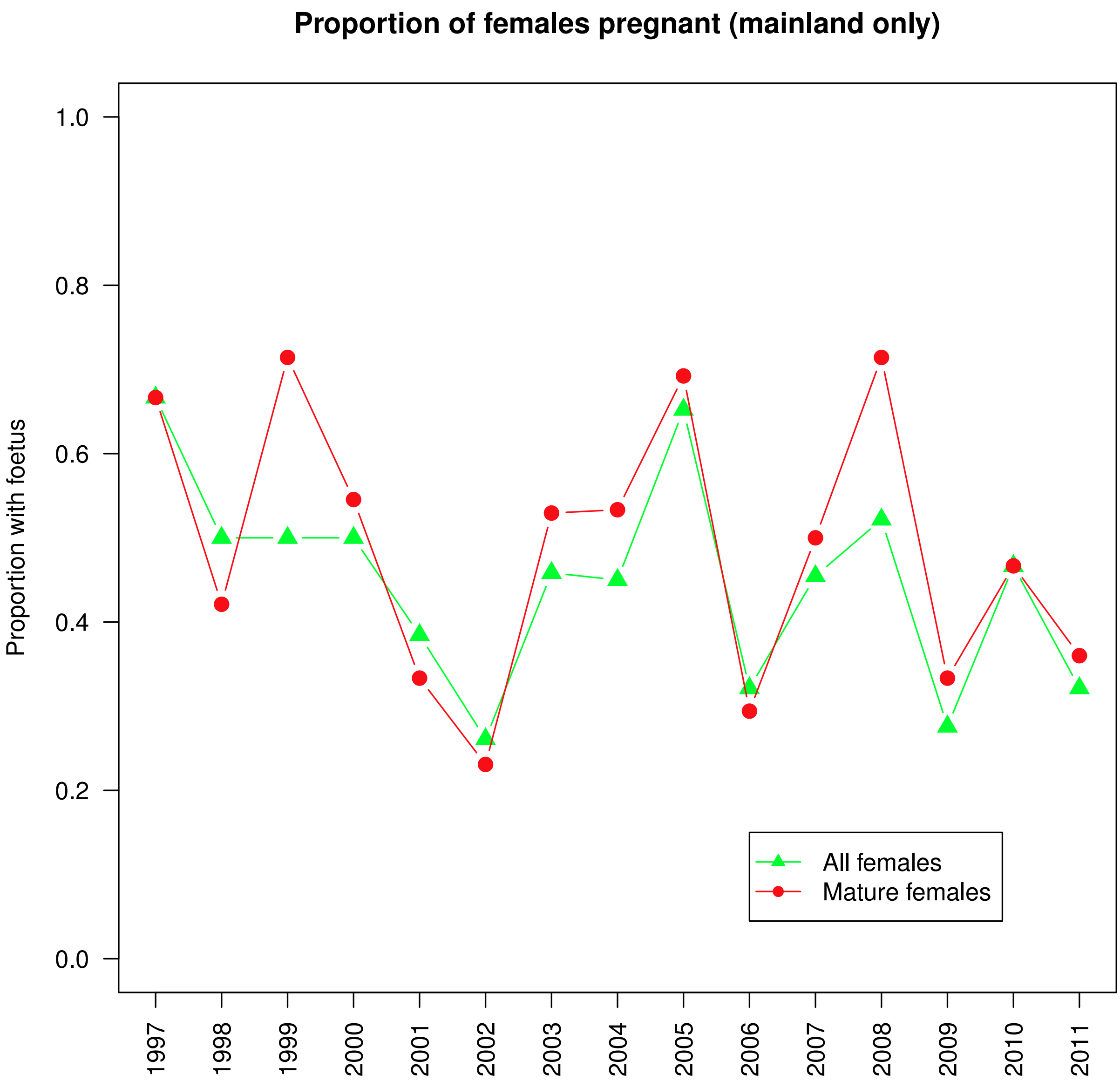


Figure 13. Proportion of females harvested on mainland reported as pregnant, 1997–2011. The two lines on the graph give the proportions for all females (n=332), and for mature (2 years and older) females only (n=236).

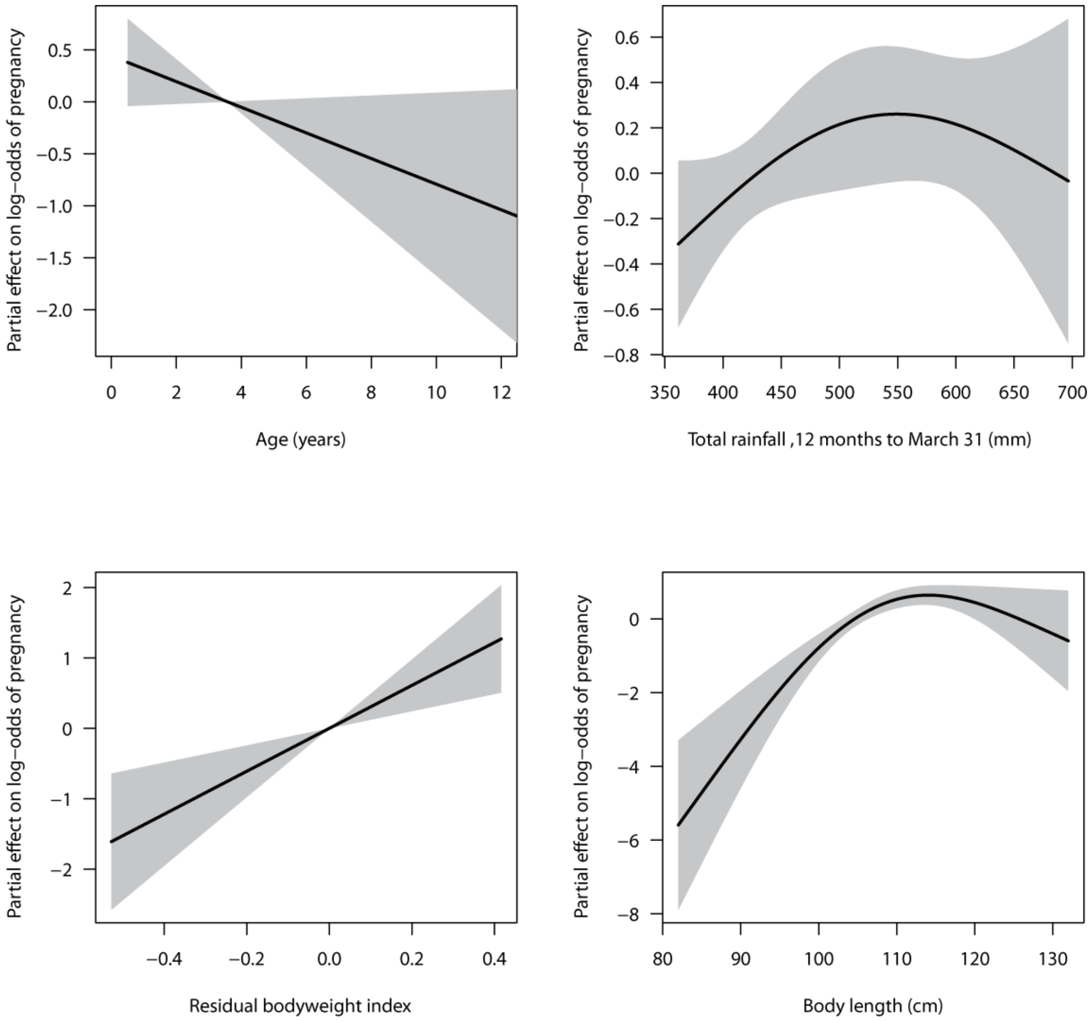


Figure 14. Graphical representation of the generalised additive model for reproductive status of females shot on the mainland, 1997–2011. Each panel shows the inferred, partial relationship between a predictor variable, and the log-odds of females being in a pregnant and/or lactating state at time of harvest, controlling for the effects of all other variables in the model. The shaded areas are the standard errors on the inferred partial effects.

3.11 Antler length

A generalised additive model was used to infer the potentially non-linear effects of age, body length, residual body weight and rainfall in the 12 months preceding the hunting season on the length of each male's longest antler (Figure 15, Table 3). Lengths of antlers increased linearly with body lengths and residual body weights of males (Figure 15). The effect of age on antler length increased up to an age of approximately 5–6 years, before declining somewhat amongst older males (Figure 15). The effect of rainfall on antler length was non-significant (Figure 15, Table 3).

Table 3. Summary of the smoothing terms included in the generalised additive model of the antler lengths of harvested Hog Deer (n = 761). The adjusted r^2 for the model was 0.771.

Parameter	df[1]	F-statistic	P-value
Age	1.988	605.627	<0.0001
Rainfall	1.719	1.394	0.25
Residual body weight	1.000	45.612	<0.0001
Body length	1.552	64.964	<0.0001

[1]Effective degrees of freedom

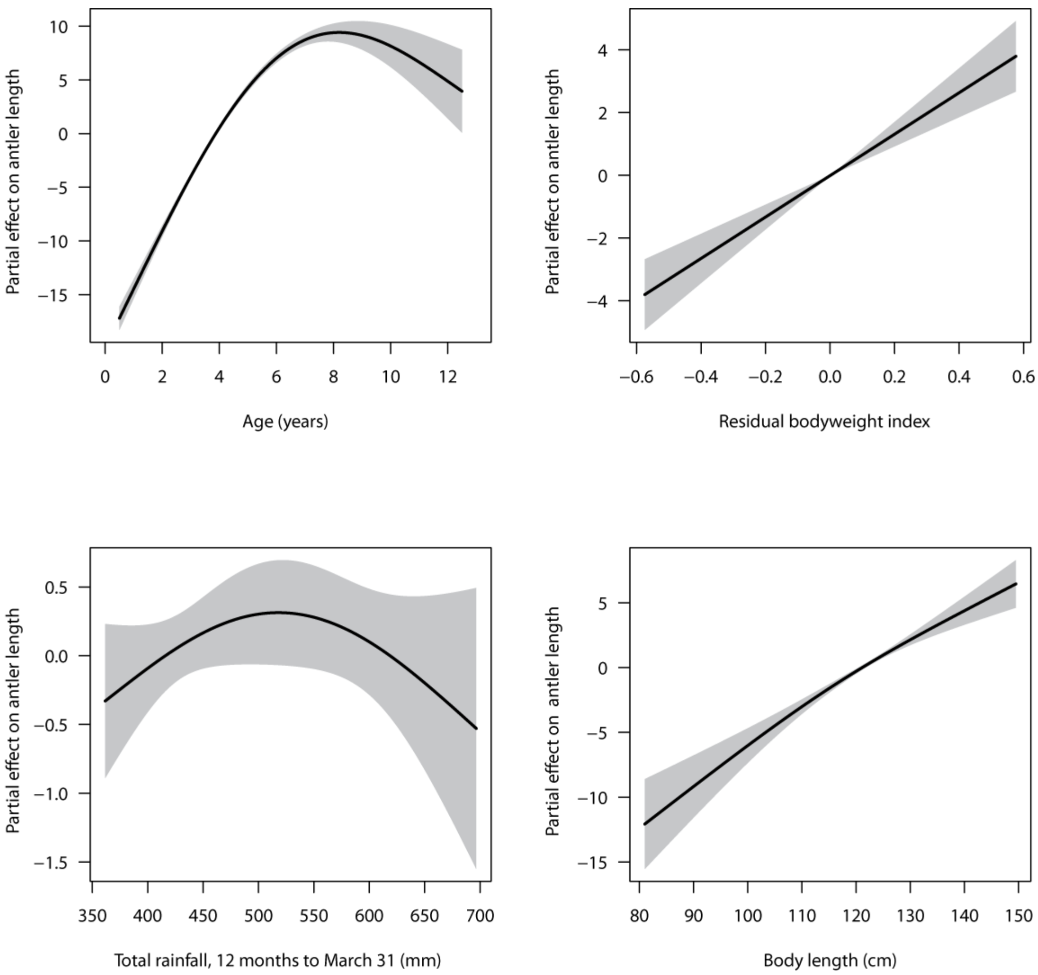


Figure 15. Graphical representation of the generalised additive model for length of antlers of males shot on the mainland, 1997–2011. Each panel shows the inferred, partial relationship between a predictor variable, and the length of antlers at the time of harvest, controlling for the effects of all other variables in the model. The shaded areas are the standard errors on the inferred partial effects. Antler length for each deer was defined as the length of the longest antler.

3.12 Antler spread

Antler spread increased with age, although there were few data for older age classes (6+; Figure 16). There was no evidence of a relationship between antler spread and longitude (Figure 16), suggesting that the hypothesis of variation in antler spread from east to west is not supported by the available harvest data.

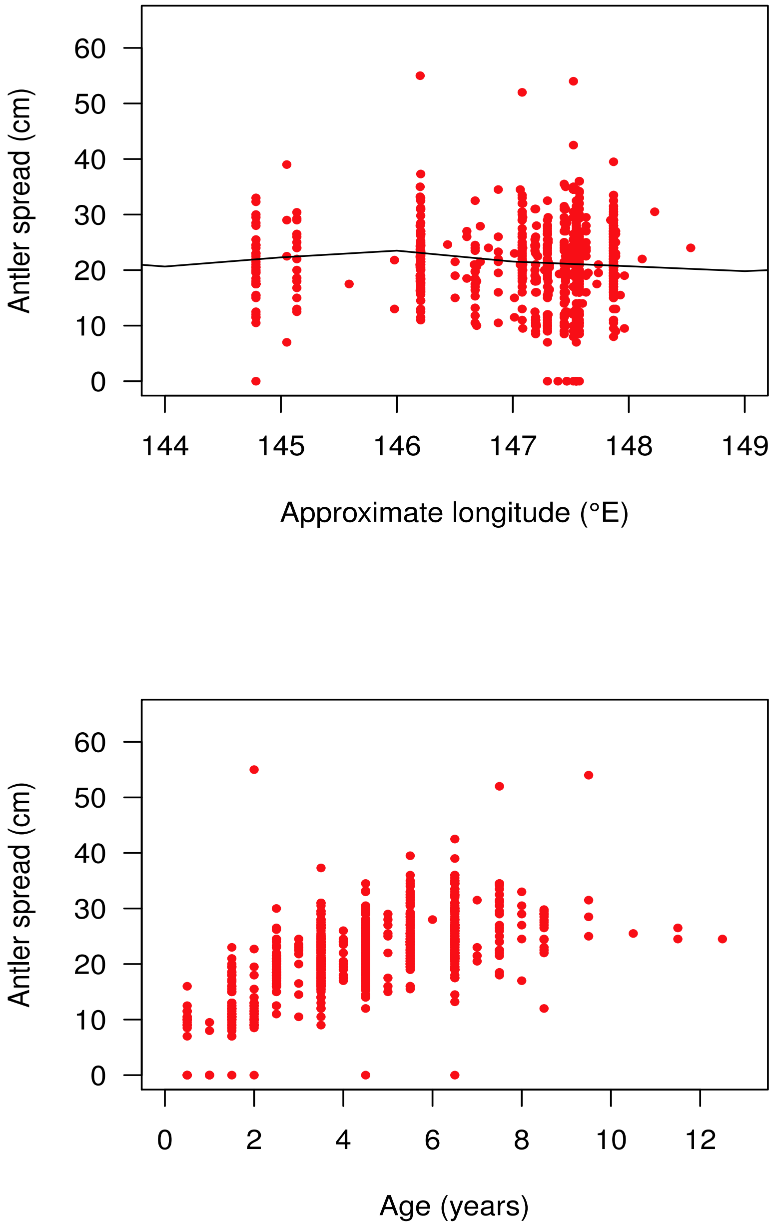


Figure 16. (Top) Relationship between antler spread and longitude of harvest location for male Hog Deer harvested on the mainland, 1997–2011. The overlaid solid line is a locally weighted least-squares regression line. (Bottom) Relationship between antler spread and estimated age for males shot on the mainland, 1997–2011

3.13 Antler asymmetry

The influence of age, body weight, body length and rainfall on the asymmetry of antlers of harvested males was also assessed using a generalised additive model, as for the models of antler length and reproductive status described above. Overall, asymmetry of males' antlers increased linearly with age and body length (Table 4, Figure 17). The effect of residual body weight index on antler asymmetry was marginally non-significant (p=0.07, Table 4), and predicted more asymmetrical antlers in males with lower-than-average residual body weights. The influence of rainfall on asymmetry of antler was weak and statistically non-significant. Overall, the statistical model for antler asymmetry was only weakly predictive, and explained relatively little of the overall variation in male antler symmetry (r^2= 0.027, Table 4).

Table 4. Summary of the smoothing terms included in the generalised additive model of antler asymmetry in harvested Hog Deer (n = 761). The adjusted r^2 for the model was 0.0269.

Parameter	df[1]	F-statistic	P-value
Age	1.000	3.923	0.048
Rainfall	1.000	1.394	0.66
Residual body weight	1.747	45.612	0.07
Body length	1.000	64.964	0.02

[1]Effective degrees of freedom.

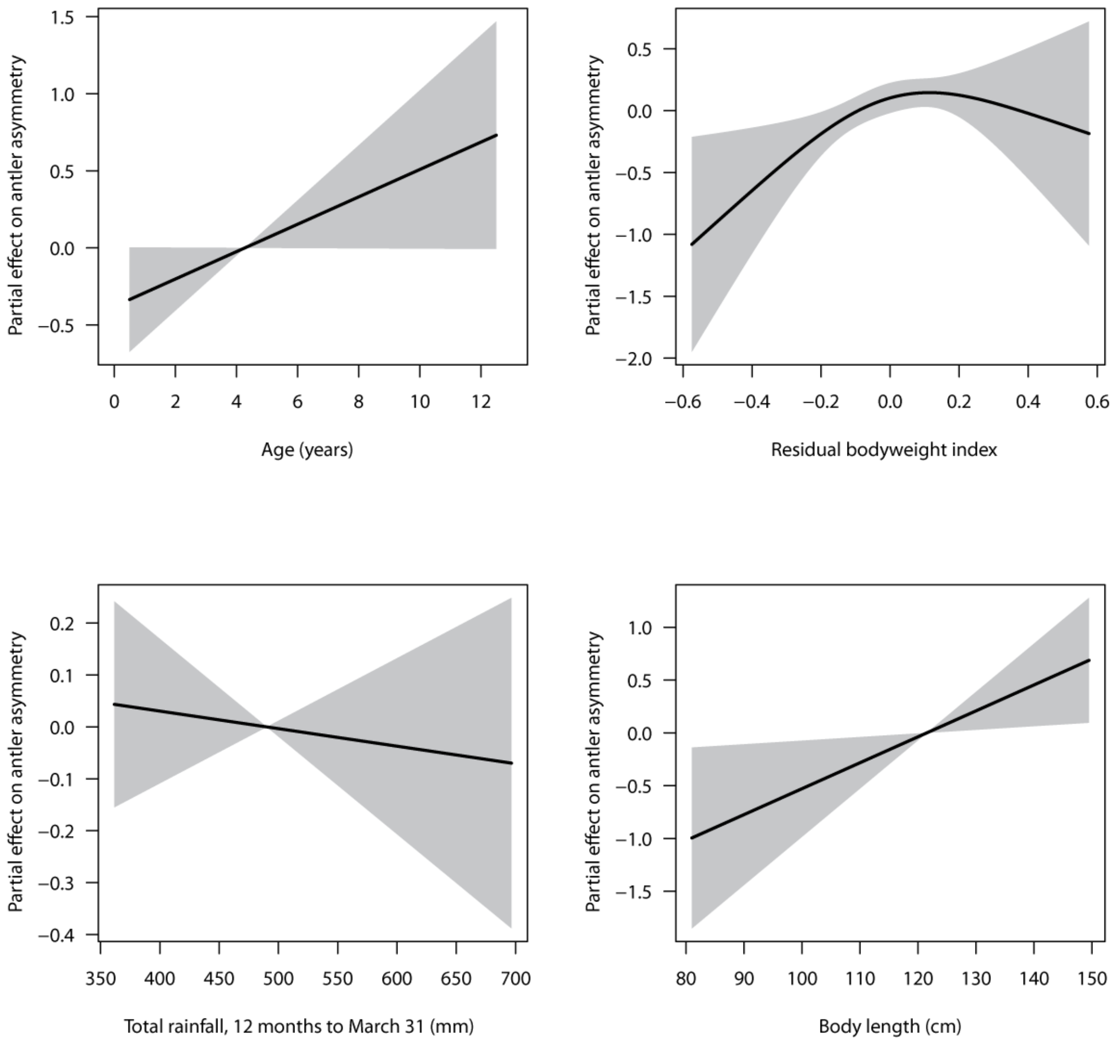


Figure 17. Graphical representation of the generalised additive model for the asymmetry of antlers of males shot on the mainland, 1997–2011. Each panel shows the inferred, partial relationship between a predictor variable, and the asymmetry of antlers at the time of harvest, controlling for the effects of all other variables in the model. The shaded areas are the standard errors on the inferred partial effects. Antler asymmetry was defined as the absolute value of the difference between the lengths of each male's antlers.

3.14 Hunter selectivity for large-antlered males

We hypothesised that within hunting seasons, hunters might preferentially harvest males with the longest antlers (i.e. 'trophies'). If the supply of large-antlered males is limited, then it would be expected that the longest-antlered males would be more likely to be harvested early in the season, when availability is maximal, and hunting effort is probably also highest. Later in the season, hunters might be expected to become less selective as the supply of preferred trophy males becomes depleted and available hunting days decline. We evaluated this 'hunter selectivity hypothesis' by computing the Spearman rank correlation between the within-season ranks of antler lengths and the day of April on which each male was shot. Contrary to our predictions, the data showed little evidence of selective shooting of large-antlered males early in the season: the Spearman rank correlation only differed significantly from zero in one (2006) of the 15 years of data included in the analysis (Figure 18).

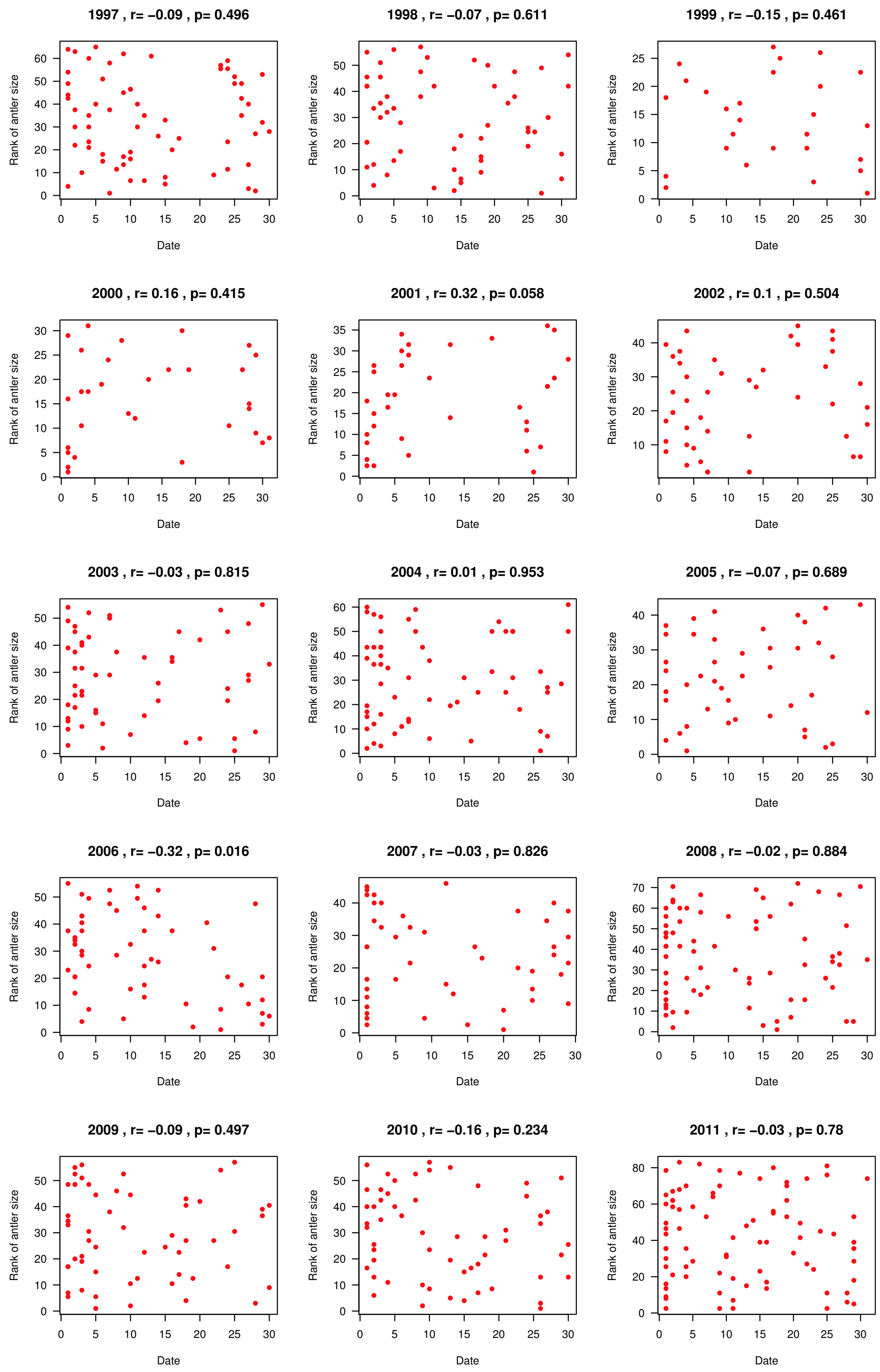


Figure 18. Relationships between within-season ranks of antler lengths of harvested males, and the dates of harvesting. If hunters preferentially target large-antlered males, then a negative relationship between rank antler length and date of harvest is to expected. The sign and significance of the Spearman rank correlation coefficient (denoted r) provides a statistical test of this hypothesis for each year of the study.

4 Discussion

4.1 Harvest statistics

Between 700 and 800 hunters have been issued with Hog Deer tags annually during 1997–2011 (DSE, unpublished data), suggesting that annual hunting effort for this species has remained approximately constant during this period. The absence of significant temporal trends in annual Hog Deer harvest size, sex ratio, age structure and female reproductive condition together suggest that the abundance and sex-age class structure of the Hog Deer population has not changed substantially during 1997–2011. It important to note that illegal harvesting of Hog Deer also occurs – as illegal harvesting is often not reported, the total annual harvest of Hog Deer in Victoria will be higher than the legal harvest statistics reported here.

4.2 Timing of harvest

More Hog Deer were harvested on the first day of the hunting season (i.e. 1 April) than any other day. We interpret this as a combination of animals being relatively naïve at the start of the hunting season following 11 months without legal hunting, making finding and killing deer easier for hunters than otherwise, and hunting effort being greatest on the first day of the hunting season.

The majority of deer were harvested in the hours around dawn and dusk, particularly on the mainland. Hog Deer are diurnal in their native range (Tak and Lamba 1981), but observations on Sunday Island indicate that they become more crepuscular and nocturnal after the hunting season begins (Mayze and Moore 1990). Such learned behavioural responses to hunting pressure likely explain the harvest peak in the first three days of the season, and at dawn and dusk.

The slightly different pattern of harvest timing observed on Sunday Island compared to the mainland is probably reflective of the different motivations and hunting activity patterns of Sunday Island hunters. As hunters on Sunday Island are nearly all non-residents who travel to the island to hunt, the finding that hunting activity is more spread throughout the day than on the mainland is unsurprising: having invested in travelling to the island, these hunters may spend many of the hours of daylight hunting so as to maximise their success, rather than confining themselves to shorter bouts of hunting around dawn and dusk, despite hunting at dawn and dusk likely being more efficient.

4.3 Age structure

Interpretation of age structure from the harvested deer is problematic for several reasons. Firstly, the extent to which age estimates are subject to error is essentially unknown. While tooth wear and eruption is widely used as an indicator of age for a variety of domestic and wild ungulates, the resulting age estimates will often be inaccurate (Fraser and Sweetapple 1993; Hamlin et al. 2000). In particular, discriminating the ages of older animals is less accurate because all teeth have erupted and increasing levels of tooth wear become less age-specific. Alternative methods of age-determination such as eye-lens analysis (Connolly et al. 1969), or examination of annular growth marks in tooth cementum (Asmus and Weckerly 2011), may yield more accurate estimates of the ages of individual Hog Deer (see 'Recommendations' below). There appears to have been inconsistency in the way that the ages of harvested Hog Deer were estimated. For Hog Deer harvested on Sunday Island, ages greater than 5 years were all recorded as one '5+' category. In contrast, ages of animals harvested on the mainland were estimated at up to 12 years old. Notwithstanding the apparent inconsistencies in the way that ages were estimated and reported, the age structures of harvested deer (Figure 8) indicate that relatively few first-year deer are harvested on the mainland, possibly reflecting avoidance of this youngest age class by hunters. Secondly, the age structure of the harvested population is likely to be a biased sample of the population due to hunter preferences (e.g. for trophy males rather than young-of-the-year) and differential vulnerability of age and sex classes (e.g. younger animals may be easier to harvest than older animals as they have less experience of hunters).

Notwithstanding the above caveats, the age structures of male and female Hog Deer harvested on the mainland showed some differences (Figure 8). Fewer males in the 0–1 year age class were harvested relative to both females in the 0–1 year age class and males in the each of the 1–7 year age classes. The apparent preference of hunters for males aged older than 1 year is likely due to hunters' preference for males with antlers (Mayze and Moore 1990). The very low numbers of males and females older than 7 years is likely due to their rarity in the population due to natural and hunting mortality.

4.4 Shoulder height and body length

As expected, shoulder height increased with body length for male and female deer (Figure 11). Males had greater shoulder heights and body lengths than females, although there was some overlap between the sexes (Figure 11).

4.5 Body condition

At a given body length, males were heavier than females, consistent with previous studies of Hog Deer in Victoria (Mayze and Moore 1990), and similar to the patterns observed in many other ungulates (Weckerly 1998). The body condition (measured using the residual body mass index) of males—but not females—varied between years and was significantly greater following a year of high rainfall. Such a relationship was likely caused by the increased quality and quantity of food (particularly pasture grasses; Davis et al. 2008) during wetter years. Positive effects of increasing food availability on body condition have been reported in several other ungulate populations (e.g. Choquenot 1991), so this result was unsurprising. Bourgarel et al. (2002) also found a stronger relationship between rainfall and condition for males than females, and attributed this finding to males being generally more susceptible to variation in resource abundance than females (e.g. Owen-Smith 1993).

The generally lower than long-term average rainfall conditions that occurred during the study (i.e. 1991–2011, Figure 3) may have reduced the availability of food resources below those that have historically applied to the Gippsland Hog Deer population. If that was the case, then the body condition indices observed during this study may have been lower than would be observed during periods of higher rainfall.

4.6 Female reproductive status

Females that were longer and had a higher residual body condition index were more likely to be in reproductive condition (i.e. pregnant or lactating) than those that were shorter and had a lower body condition index (Figure 14, Table 2). The effects of rainfall and age on the probability that females were in reproductive condition were comparatively weak after the effects of body size and body condition were accounted for. Given the physiological costs of pregnancy and lactation, it is unsurprising that reproduction is more likely in larger and proportionally heavier females, and such effects have been previously reported in a variety of ungulate species (e.g. Albon et al. 1986; Testa and Adams 1998; Gaillard et al. 2008).

4.7 Antler length, spread and asymmetry

The antlers of male deer act as both weapons in male–male competition and as signals of 'quality' to potential mates (Clutton-Brock 1982; Bartoš and Bahbouh 2006). Male Hog Deer first grow antlers in their second year and continue to renew them annually until they die (Mayze and Moore 1990). We found that males with larger body lengths, and those with higher residual body weight indices, had longer antlers, which is consistent with findings for other deer species (e.g. Red Deer *Cervus elaphus*; Bartoš and Bahbouh 2006; Mateos et al. 2008). At a given size and weight, younger males had smaller antlers, except for the very oldest age classes (>8 years) in which antler length began to decline, possibly indicating senescence amongst these older age classes (Figure 15). Declining antler sizes in the oldest age classes have also been observed in other deer species (e.g. Roe Deer *Capreolus capreolus*; Mysterud et al. 2006).

Contrary to our predictions, there was no evidence that antler spread of harvested males varied systematically across the species' geographic range in Victoria (Figure 16). Antler spread generally increased with age, at least until males were approximately 6 years old: there were few data for older males, meaning that trends in antler spread for older males could not be reliably inferred.

Asymmetry of antlers was less predictable than antler length, with asymmetry increasing slightly with body length and age. Given that symmetry of secondary sexual characteristics is predicted to be positively associated with measures of health and physiological vigour such as body size and condition, this result is counter-intuitive. It is possible that greater levels of asymmetry in the antlers of larger Hog Deer might in many cases be attributable to breakage of a single antler, rather than inherent asymmetry in the growth of the antlers themselves. If larger, heavier deer have larger antlers and engage in more frequent combat, or are more prone to other sources of antler damage, than smaller, lighter deer, then a greater frequency of antler breakage might be expected, and might partially explain the counter-intuitive finding of greater antler asymmetry in larger Hog Deer.

The harvest data provided no support for the hypothesis that hunters would preferentially harvest, and hence deplete, the supply of large-antlered males during the early part of the annual hunting season. This conclusion is consistent with the notion that although hunters may prefer to harvest large-antler males, they may be unwilling to forgo harvesting less-preferred males in the hope of subsequently harvesting a more preferred large-antlered individual or the availability of hunting opportunities may limit their opportunities to realise this preference.

5 Recommendations

Our analyses indicate the usefulness of the data that has been collected from Hog Deer at checking stations since 1997 for improving our understanding of the Victorian Hog Deer population. We make two specific recommendations that would enhance the value of data collected from those checking stations in future years.

5.1 Recommendation one: extract eyeballs to better estimate age

The ages of deer estimated from molar progression are accurate for animals aged up to three years (Fraser and Sweetapple 1993), but thereafter age must be estimated from tooth wear, which can be inaccurate (Hamlin et al. 2000). A more accurate method of estimating age is by eye-lens weight. Because the eye lens continues to grow until death (Smith 1883; Krause 1934; Augusteyn 2007a), the weight of the eye lens has commonly been used to estimate the age of mammalian species since the 1950s (e.g. Lord 1959; Dudzinski and Mykytowycz 1961; Longhurst 1964; Connolly et al. 1968; Feldhamer and Chapman 1980; Augusteyn 2007b). Unlike tooth wear (Hamlin et al. 2000), the growth of the lens is thought to be unaffected by nutritional factors (Kauffman and Norton 1966; Friend 1967), but may vary with gender (R.C. Augusteyn, pers. comm.). Because the weight of the lens may change rapidly post-mortem, the dry weight of lenses fixed in 95% ethanol is used as the predictor of age. The relationship between eye-lens weight and age has been investigated for Hog Deer using animals tagged as calves and subsequently harvested (i.e. of known age) on Sunday Island (D.M. Forsyth et al., unpublished data) and could be used to predict the age of harvested animals in which molar progression has ended (i.e. older than three years).

We therefore recommend that the left and right eyeballs be extracted from all Hog Deer presented at checking stations. The lenses should be stored separately, completely covered in 95% ethanol, in individually labelled containers. The containers should also be labelled with ‘left’ or ‘right’ for the respective eyeball. After the hunting season, the lenses should be oven dried to a constant weight, and the age predicted from the known, parameterised relationships between lens weight and age. A protocol, and training of checking station operators, could be provided by the Arthur Rylah Institute for Environmental Research. Continued recovery of eyeballs from tagged deer of known age from the Sunday Island population will allow refinement of the accuracy of the eye-lens aging protocol over time.

5.2 Recommendation two: measure the weights of the kidney and kidney fat

We used the residuals from the sex-specific relationship between body length and weight as our measure of body condition. However, fat is the body component most often associated with body condition (Pond 1977) and is likely to be more responsive to environmental changes (e.g. forage availability) than the residual body weight index we used to assess body condition. Riney’s kidney fat index (KFI; Riney 1955) is one of the most frequently used indices of fat reserves and of general physical condition (Torbit et al. 1988), and is straightforward to measure.

We therefore recommend that the weight ($\pm$ 0.5g) of the right kidney (or left kidney if the right is damaged or unavailable) with and without the fat surrounding the kidney be measured. To avoid inclusion of mesenteric fat, fat extending beyond the end of the kidney should not be weighed. Following Riney (1955), the KFI can then be calculated as 100 $\times$ the mass of fat surrounding the kidney divided by kidney mass. Collection of the KFI will facilitate more thorough and reliable analysis of variation in body condition of deer. A protocol, and training of checking station operators, could also be provided by the Arthur Rylah Institute for Environmental Research for this technique.

5.3 Other recommendations

Our analyses have shown that the checking station data are useful for evaluating changes in aspects of the harvest and the harvested animals. However, the limitations of these data should be recognised. First, it is difficult to interpret total harvest in terms of underlying population dynamics without reliable data on hunting effort and / or independent estimates of deer abundance. Increases or decreases in annual legal harvest may reflect increases or decreases in hunting effort, deer abundance or both. We have therefore largely refrained from making statements about trends in the underlying population, instead restricting our statements to the legal harvest.

The most robust way of inferring the population dynamics of Hog Deer in Victoria would be to conduct unbiased sampling of the wild population. The sampling could be done using a variety of methods, including annual spotlight counts in a subsample of locations, as is currently undertaken on Sunday Island by the Para Park Co-operative Game Reserve Limited. Spotlight counts also have the advantage of allowing animals to be classified by sex and age classes, such that changes in abundance of classes can be separately discerned from the data, notwithstanding any differences in detectability of different groups. For example, the estimated female:fawn ratios obtained from spotlight surveys would be informative with respect to variation in Hog Deer reproductive rates between areas and years, and also in response to factors such as Red Fox (*Vulpes vulpes*) baiting. Estimating the abundance of adult male Hog Deer might also aid with setting more localised Hog Deer harvests. A spotlighting protocol, assistance with selecting sites for spotlight transects, and interpretation and analysis of any resulting data could be provided by the Arthur Rylah Institute for Environmental Research.

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