Estimating Kaimanawa feral horse population size and growth

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ABSTRACT

Animal flight behaviour in response to aircraft could have a profound influence on the accuracy and precision of aerial estimates of population size but is rarely investigated. Using independent observers on the ground and in the air we recorded the presence and behaviour of 17 groups, including 136 individually marked horses, during a helicopter count in New Zealand's Kaimanawa Mountains. We also compared the helicopter count with ground-based estimates using mark-resight and line-transect methods in areas ranging from 20.5 to 176 km^2. Helicopter counts were from 16% smaller to 54% larger than ground-based estimates. The helicopter induced a flight response in all horse groups monitored. During flight, horse groups traveled from 0.1 up to 2.75 km before leaving the ground observer's view and temporarily changed in size and composition. A tenth of the horses were not counted and a quarter counted twice. A further 23 (17%) may have been counted twice but only two of the three observers' records concurred. Thus, the helicopter count over-estimated the marked sub-population by at least 15% and possibly by up to 32%. The net over-estimate of the marked sub-population corresponded to the 17% and 13% difference between helicopter counts and ground-based estimates in the central study area and for the largest area sampled, respectively. Feral horse flight behaviour should be considered when designing methods for population monitoring using aircraft. We identify the characteristics of the helicopter count that motivated horse flight behaviour. We compared our own recent estimate of population growth from measures of fecundity and mortality (λ = 1.096 with an earlier-published one (λ = 1.182, where r = 0.167) that had been derived by interpolating between the available history of single counts. Our model of population growth, standardised aerial counts, and historical estimates of annual reproduction suggest that the historical sequence of counts since 1979 probably over-estimated growth because count techniques improved and greater effort was expended in successive counts. We used line-transect, mark-resight and dung density sampling methods for population monitoring and discuss their advantages and limitations over helicopter counts.

1. Assessment of current helicopter counts for estimating population size

1.1 INTRODUCTION

Population estimates are seldom exact. The best that wildlife managers can expect is to know that the size of the population probably falls between two values that are defined by measures of estimate variation and statistical confidence. It would also be advantageous to understand why, and by how much, an estimate might vary from the true value. With this understanding methods may be refined and standardised to reduce sources of variation that are associated with technique or circumstance, rather than population size. Also, when sources of error are known and estimated, real changes in population size can be distinguished from differences that result from estimate error. Good population estimates combine accuracy with precision. An estimate is accurate when it is close to the true value; an estimate is precise when replicated estimates yield a similar result. In most circumstances, estimates with poor accuracy are only useful if the estimate's deviation from the true value can be reliably approximated. Precision is particularly important if different estimates are to be compared to detect trends in population size.

The use of aircraft for estimating population size is commonplace (Seber 1992) but how they are used varies regionally (New Zealand—Rogers 1991; Australia—Caughley & Grice 1982, Hone 1988, Pople *et al.* 1998; North America—Gasaway *et al.* 1985, Bodie *et al.* 1995, Bowden & Kufeld 1995, Pojar *et al.* 1995). The accuracy and precision of aerial population estimates varies with observer experience, aircraft type and altitude, weather conditions, season, vegetation, and animal activity, mobility, grouping and orientation (e.g. Caughley 1974, Frei *et al.* 1979, Kufeld *et al.* 1980, Gasaway *et al.* 1985, Wolfe 1986, Bleich *et al.* 1990, Bodie *et al.* 1995). Thus, there are numerous potential sources of error in aerial estimates of population size. In particular, the behavioural response of the animals to being counted from the air is less often investigated than the other factors that effect count accuracy and precision. Nevertheless, whether animals characteristically seek or break from cover, freeze or take flight, and disperse or group together in response to an aircraft, may have a profound effect on population estimates (Seber 1992; e.g. Bleich *et al.* 1990). The anti-predator behaviour of the horse is characterized by grouping and flight. Thus, if disturbed by aircraft, feral horses tend to break from cover if they are in it, run, and form into larger aggregations. The implications of feral horse anti-predator behaviour for aerial estimate accuracy and precision has not been studied.

Aerial counting is the direct counting of a population, usually from a small aeroplane or helicopter, *in lieu* of a population census (Seber 1992). Aerial counting is not a sampling regime unless counts are replicated (Harris 1986) but counts are seldom replicated. Thus, counts are not usually complemented with measures of sample variability that can be used to obtain population estimates with diagnostic and statistical measures of reliability and confidence. Therefore, aerial counting should not be equated with more rigorous and repeatable methods such as distance sampling using line or strip transects (Buckland *et al.* 1993; e.g. Hone 1988) or mark-resight (Pollock 1991; e.g. Bowden & Kufeld 1995) methods that are also conducted from the air. However, neither is an aerial count a population census, according to the proper statistical use of the term ('The complete enumeration of a population...': Marriott 1990), although this is how they are often termed (e.g. Rogers 1991; Symanski 1996). A significant proportion of the population may be missed or counted twice and, therefore, estimates may deviate dramatically from the true number (Harris 1986; e.g. 41–112% of true population size: Garrott *et al.* 1991a). Managers can improve the precision of counts by using the same methods (e.g. aircraft type and technique) consistently between counts and by conducting them in similar circumstances (e.g. weather) each time. It is more difficult to assess count accuracy unless true population size is known. Nevertheless, at least two other population estimates that use different methods, and that themselves yield similar results, might be used to judge count accuracy.

Department of Conservation (DOC) aerial counts of Kaimanawa horses have been disputed (Wright 1989; Coddington 1991). DOC counts were designed to produce a single absolute number for population size and have been referred to as a helicopter 'census' (Rogers 1991, DOC 1995). Count methods have been gradually refined since the first in 1986 and, therefore, their accuracy is likely to have changed. Attempts to standardise count methods since 1994 have resulted in better consistency of technique between counts (DOC 1995) and perhaps improved count precision. Nevertheless, the accuracy and precision of the counts is not known. It has been suggested that counts under-estimated population size by 10 to 20% (Rogers 1991). We investigated the influence of feral horse anti-predator behaviour on a helicopter count conducted in New Zealand's Kaimanawa Mountains.

1.2 METHODS

Study animal and area

The origins, size, behaviour and ecology of the Kaimanawa feral horse, and the vegetation, topography and climate of its range, are described in detail by Cameron *et al.* (2001; see also Linklater *et al.* 2000). Horses were reliably identified by two adjacent 2" × 3" freeze brands on their dorsal right rump and/or by documented variations in their coloration and white markings. Bands were identified by their marked and stable membership (Cameron *et al.* 2001).

Observations of the helicopter count and horse behaviour

The helicopter count was conducted from a Hughes 500 helicopter. The Kaimanawa feral horse range was divided into count strata based loosely on water catchments and delineated by geographical features such as escarpments, rivers and mountain ridges. The horses in each stratum were counted by flying approximately parallel paths backward and forward across each stratum, moving from one path to the next adjacent path in sequence. In this way the helicopter moved systematically in a serpentine pattern beginning at one side of each stratum and ending at the opposite side in an attempt to count all horses present. The helicopter was guided by a global positioning system and paths were 300 or 500 meters apart. The 300-m spacing between paths was used where densities were perceived to be highest. The helicopter was flown at approximately 60 knots ground speed and at approximately 60 metres above the ground.

Counters

Two counters in the helicopter were linked by two-way intercom and when a group of horses was seen they counted the number in the group. If necessary, they requested the pilot to circle a group of horses so that group size could be confirmed. Counters gave each group a unique number and marked its location on a 1 : 50 000 scale topographical map (DOC 1997).

Aerial observer

The aerial observer was in the helicopter during the count. This observer also recorded the DOC number for each group along with the location and size of any marked bands that they were able to identify from the helicopter, as it passed near or over them, and whether or not they were counted. The ground and aerial observers, but not the counters, were familiar with the unique marks of individual horses in the population from previous work (e.g. Cameron 1998; Linklater 1998). The aerial observers and counters could communicate by intercom but the aerial observer did not contribute to the counting of horses and used the intercom only to confirm with the counters the groups they counted, their unique identification number and their size.

Ground observer

Immediately prior to the helicopter count the ground observer recorded the location coordinates and size of marked bands and individual horses in the Argo Basin (the central study area, see Cameron *et al.* 2001) on a 1 : 25 000 scale topographical map. The observer obtained a vantage with an approximately 300° view at 250 m altitude above the Basin's floor, which allowed him or her to follow the movement of those horses during the helicopter count. He or she recorded the horses behaviours and movements, and their locations (on 1 : 25 000 scale topographical map) during the helicopter count.

Horse counting

i. When the composition and location of a horse group as recorded by ground and aerial observers as the helicopter flew over it concurred, but the group was not counted, then the group was confirmed to have not been counted.

ii. When a marked group of horses was identified by the aerial observer under the helicopter more than once and it was heard to be counted on each occasion, then a double count was recorded. The double count was confirmed only if the records from the three observers concurred as to the identity and location of the marked group when it was counted on both occasions. The records of the movement and location of each horse group made by the ground and aerial observers were compared to confirm each group's identity on both occasions that it was counted. If the location and size of the group as recorded by the counters and aerial observer also concurred, then it was confirmed that the same group was counted on each occasion that the helicopter flew over it.

iii. When the records of the location and composition of a group of horses by aerial and ground observers concurred, on both occasions that it was counted, but this location did not concur with that recorded by the counters, it was regarded as an unconfirmed double count.

Line-transect and mark-resight population estimates

We used line-transect and mark-resight methods to estimate population size within strata also counted from the helicopter. The line-transect and mark-resight techniques used are described in detail in Cameron *et al.* (2001, see also Chapter 3, present study). In brief, 10 line transects, placed across the southern half of the Kaimanawa wild horse range in the Auahitotara ecological sector, were negotiated on a motorized all terrain vehicle (A.T.V.; 4 wheel drive, 300cc motorbike). The Auahitotara ecological sector was divided into the Southern Moawhango (SM), Hautapu (H) and Waitangi (W) zones that included 3, 3, and 4 of the transects, respectively (see Fig. 1 in Linklater *et al.* 2000 or Fig. 3 in Cameron *et al.* 2001). Line transects were conducted in mid-autumn (April) 1996 after the foaling season and when >85% of foal mortality for the year had already occurred (Cameron 1998).

During transects the locations of horse groups detected with the naked eye were recorded on 1 : 25 000 scale topographical maps. Perpendicular distances between the horse group and the line transect were determined by measuring the distance between the horse group and the line transect as marked on the map. The perpendicular distances and group size were entered into the DISTANCE line-transect software (Laake *et al.* 1994) to estimate horse density. The Fourier series with truncation where $g(x) = 0.15$ and grouping of the perpendicular measures into even intervals (SM $n = 4$, H $n = 7$, W $n = 10$ intervals) were used to construct the detection functions. The best number of even intervals for grouping of perpendicular distances, and level of truncation, were determined retrospectively to minimize the estimates' co-efficient of variation and remove distance clumping effects. The estimation process checked for a relationship between group size and visibility from the line transect. Significant relationships were not found and so average group size was used to estimate density from the number of groups and their distance from the line transect. In this way population size estimates and their 95% confidence intervals were calculated using 1000 bootstraps of the density estimation process (Buckland *et al.* 1993; Laake *et al.* 1994).

The location of marked breeding groups inside or outside the Argo Basin mark-resight area was known from regular band relocation events every 9 days (average, range 3 to 21 days) during the entire study (Cameron *et al.* 2001). Therefore, closed population mark-resight techniques could be used. A resight event was conducted in the Argo Basin on 25 April 1996, during the same period as the line transects, and on 25 July 1996, two days prior to the helicopter count. We walked a circular route through the northern and southern halves of the Argo Basin, recording the size of all groups of horses and the identities of marked individuals in them. Population estimates for the Argo Basin were calculated from estimates of the number of bands using NORMARK mark-resight software (White 1996) and the average size of marked and unmarked bands observed and not observed.

The outermost coordinates of groups of horses recorded from the line transects within different zones and mark-resight routes on 5 and 38 other occasions respectively (Cameron *et al.* 2001) were used to construct minimum convex polygon (m.c.p.) templates of the areas they sampled. The minimum convex polygons were constructed using sightings of 889 groups in the Argo Basin mark-resight area, 382 in the Southern Moawhango zone, 98 in the Hautapu zone, 62 in the Waitangi zone, and 542 in the Auahitotara ecological sector. The area sampled is defined in this way because the m.c.p. around the perimeter of the bands sighted is representative of the extreme values of the detection function and, thus, describes the area that they sample from. The calculated density of horses within line-transect templates was multiplied by the size of each template to obtain an estimate of the number of horses. The number of horses counted from the helicopter within the boundaries of the different line-transect and mark-resight templates was determined by overlaying the templates on a copy of the map on which counted bands were marked during the helicopter count.

Line-transect and mark-resight population estimates conducted within the Argo Basin template in April 1996 were compared to check for consistency in the results of the two methods. To do this the three line transects of the Southern Moawhango template that also crossed the Argo Basin mark-resight template were truncated at its borders and horse densities re-calculated as for other transects.

1.3 RESULTS

Before the helicopter count, the ground observer located and confirmed the identity of 17 marked groups in the Argo Basin. The aerial observer identified and recorded the locations of 21 marked groups during the helicopter count of the entire study area. Observations by the ground and aerial observers show that the helicopter induced a flight response that included running, in all 17 of the groups monitored by both observers (Table 1). During flight, horse groups traveled an average linear distance of 1 km and up to 2.75 km and crossed an average of 3.5 helicopter paths and up to 10 helicopter paths. These are minimum estimates of distances traveled because the majority of horse groups disappeared from the ground observer's view still running from the helicopter. Fifteen (88%) of the groups traveled far enough to move across into adjacent helicopter paths. Six (35%) of the groups crossed into an adjacent counting strata. The composition of thirteen (76%) groups changed during the helicopter count by mixing with, and separating from, other groups with the consequent temporary gain or loss of individuals (Table 1).

Comparisons between the records of the three observers show that, of the 136 marked horses located immediately prior to the helicopter count, 34 (25%) were counted more than once, a further 23 (17%) may have been counted more

TABLE 1. MOVEMENT AND MEMBERSHIP CHANGE OF MARKED HORSE GROUPS IN THE ARGO BASIN DURING THEIR FLIGHT RESPONSE TO THE HELICOPTER COUNT. nd = NO DATA.

GROUP	LINEAR DISTANCE TRAVELED (m)	NUMBER OF HELICOPTER PATHS CROSSED	DID THE GROUP MOVE BETWEEN COUNT STRATA?	DID THE GROUP'S MEMBERSHIP CHANGE?
Bachelor 1	100*	0*	No	Yes
W	150	1	No	No
Alaskans	200	2	No	No
Th'	280*	2*	No	No
Georgy	300*	1*	No	Yes
Zig-zag	300	1	Yes	Yes
Imposter's mare	510*	2*	No	Yes
Bachelor 2	900*	4*	Yes	Yes
Ally	950*	4*	No	Yes
Henry	970*	3*	No	nd
Mule	1200*	5*	No	Yes
Canadians A†	1300*	7*	No	Yes
C	1430*	5*	Yes	Yes
Hillbillys	1580*	3*	No	Yes
Canadians B†	2060*	3*	Yes	Yes
Black	2180*	10*	Yes	Yes
Rust	2750*	5*	Yes	Yes

* Minimum estimate of the distance traveled or number of helicopter lines crossed because the group disappeared from view still moving away from the helicopter

† The Canadians were in two parts prior to the helicopter count

than once, and 13 horses (9.6%) were not counted. Therefore, the helicopter count overestimated the marked sub-population by at least 21 (i.e. 34–13; 15.4%) and possibly by as many as 44 horses (i.e. 34+23–13; 32.4%).

Population size estimates for the 20.5 km^2 Argo Basin mark-resight template in April 1996 from mark-resight and line-transect methods were similar (mark-resight = 236; line transect = 221 horses; 6.6% difference). Helicopter counts were from 16% smaller to 54% larger than estimates derived by mark-resight and line-transect methods within their respective templates that ranged in size from 20.5 to 176 km^2 (Table 2). However, only in one region, the Southern Moawhango template that included the Argo Basin, did the helicopter count fall outside, or near the upper limits, of the large 95% confidence intervals of the line-transect and mark-resight estimates.

TABLE 2. COMPARISON OF THE HELICOPTER COUNT WITH MARK-RESIGHT AND LINE-TRANSECT POPULATION ESTIMATIONS FOR THE LINE-TRANSECT AND MARK-RESIGHT TEMPLATES.

TEMPLATE NAME	AREA (km^2)	METHOD	POPULATION ESTIMATE	95% CI	HELICOPTER COUNT	PERCENTAGE DEVIATION
Argo Basin	20.5	Mark-resight	195	157–234	228	+16.9
Southern Moawhango	46.1	Line transects	272	205–324	420	+54.4
Hautapu	53.5	Line transects	339	72–537	284	–16.2
Waitangi	66.6	Line transects	177	87–741	150	–15.3
Auahitotara ecological sector	176.0	Line transects	849	566–1303	961	+13.2

1.4 DISCUSSION

Three pieces of evidence are required to judge count accuracy and precision within the range. First, comparisons of the helicopter count with at least two more rigorous techniques that themselves yield similar population estimates. Second, close correspondence between the net quantity of over- or under-counting from direct observations of marked horses and the difference between the helicopter count and other population estimates. Third, observations that demonstrate how horses are missed or counted more than once during the count. We provide these pieces of evidence here. First, line-transect and mark-resight methods provided a similar result (6.6% difference) when compared for the 20.5 km^2 Argo Basin template. The helicopter count was 13% larger than our estimate from line transects over 176 km^2 that constituted approximately a third of the population's range and a half of the total population. Second, the over-estimate by the helicopter count of the Argo Basin template (i.e. 16.9%) also corresponds closely with the net over-counting of marked horses in the same area (i.e. at least 15.4%). The net over-counting in the Argo Basin corresponds closely to the difference between helicopter and line-transect estimates over the largest template (i.e. 13%). Third, observations show that horses were counted twice, and a smaller number not counted, because they took flight and groups mixed and traveled large distances in response to the helicopter.

The placement of line transects was not random (although approximately regular) but biased towards habitat that horses use most because these are coincidentally also habitats that can be negotiated on the A.T.V. vehicle used (i.e., moderate to gentle slopes and grassland; see Cameron *et al.* 2001). Some mortality (annual survivorship of adults = 97% males and 94% for females ≥ 5 years of age and still lower in younger age classes: Cameron *et al.* 2001) will have occurred between when line transects were conducted and the helicopter count 4 months, including winter, later. Consequently, if there is any bias in the line-transect estimates we expect them to over-estimate the horse density at the time of the helicopter count. The difference between line-transect and helicopter counting is therefore probably a conservative indication of the over-estimate that resulted from the helicopter count in some regions and overstates the under-estimate in others. We conclude that the helicopter counting of Kaimanawa wild horses of the type described can result in a small over-estimate of population size within different parts of the range due to double counting as a consequence of the flight behaviour of horses.

A count immediately before and after a large horse removal event can also be used to judge count accuracy (e.g. Garrott et al. 1991a). DOC counted 1697 horses in May 1997, and 621 in April 1998 that were before and after the musters in June 1997 that removed 1067 horses. These figures indicate that the 1997 count was accurate. Unfortunately, the post-muster count occurred 11 months after the muster during which time there was a full breeding season and winter. Therefore it is not a good example of the count-remove-recount method for assessing count accuracy. Nevertheless, if we assume an around 10% population growth for the year between the counts (i.e. a count immediately post muster would have yielded 621 – 62 = 559 horses) the figures indicate that the 1997 count detected around 96% of horses and resulted in a small under-estimate of population size. If growth rates were higher (as suggested in Rogers

1991) then the count underestimated by a larger amount (i.e. 93% detection for a population growth rate of 18% for the 1997/98 year). Therefore, counts of the type conducted since 1994 can also result in a small underestimate of population size and overall they may vary a small amount around the true value: sometimes a small over-estimate and for other counts a small under-estimate. Consequently, at this time we have 2 tests of the accuracy of the post-1993 count method; the DOC count-removal recount and our comparison with line-transect and mark-resight estimates. Garrott *et al.* (1991a) showed in independent count-removal recount trials on many different populations that horse detection varied dramatically between counts (i.e. from 41 to 112%). We therefore recommend further assessments of the count technique to improve confidence in the results of the first two tests. Lastly, the accuracy and precision of helicopter counts conducted prior to 1994 are not known because they used methods that are different from those assessed in the first two tests of count accuracy (see Chapter 2).

The flight behaviour of Kaimanawa horses in response to the low flying helicopter was typical of that observed in other ungulate populations where it is also known to confound reliable population estimates (e.g. Bleich *et al.* 1990). The spatial pattern of over- and under-estimation reveals the dramatic effect that horse flight behaviour can have on the accuracy of an aerial count. Differences between our population size estimates and those from the helicopter count varied widely within regions of different sizes and density. Over-estimates were more likely to occur in higher density areas and under-estimates in low-density areas, thus creating erroneously large differences in population size between adjacent regions. Also, helicopter counts in the smallest regions deviated most from our estimates in both directions. These patterns are consistent with horse flight behaviour in response to a helicopter because groups aggregated during flight and flight behaviour is contagious. At high densities the flight response of one group is more likely to motivate the flight response of other groups, thus, increasing their visibility and encounter or detection rate by counters. Therefore, flight behaviour has a greater confounding influence on count accuracy at high densities and when the area counted is small enough for changes in the distribution of horses, by grouping and flight, to result in either the double counting of groups or loss of horses from the region as it is counted. Judging the accuracy and precision of the helicopter counts for the entire horse range is not possible here because the counting of only around half of the range and population was assessed for a single count and only one count-muster-recount test exists. Nevertheless, we can conclude that:

i. the helicopter counts of the type conducted since 1994 probably do not consistently underestimate population size by 10–20% as previously suggested (Rogers 1991; DOC 1995), and

ii. comparisons between different regions from the same count are unlikely to be accurate or precise.

Thus, the variation in population size that Rogers (1991) observed between different count strata in different counts is more likely to be an artifact of feral horse flight behaviour, than evidence of unstable home ranges and the wide ranging behaviour of Kaimanawa horses as initially suggested. Measures of home range and dispersal show that Kaimanawa horses had stable home ranges and were conservative dispersers (Cameron *et al.* 2001).

Three features of the helicopter count in the Kaimanawa Mountains appeared to cause horse flight and double counting. First, adjacent helicopter paths were too close together, being 500 metres apart (300 metres apart in high-density areas). Therefore, a group of horses in flight could travel into subsequent flight paths before the helicopter could complete the previous one. Second, the helicopter moved systematically from one flight path to the next in sequence across each count stratum. Therefore, some of the groups of horses that took flight in response to it were herded into flight paths and strata not yet counted. Third, the helicopter flew around 60 metres from the ground. Low flying is likely to augment the flight response of the horses and flight behaviour prevented the easy recognition of groups that had already been counted because it resulted in changes in group size and composition as groups mixed and separated during flight. Thus, counters in a moving helicopter, unable to follow the movements of individual groups during the count, could not differentiate between counted and uncounted groups during the melee that resulted.

The helicopter counts have these characteristics because they were designed to census the population rather than sample from it to estimate population size. We think it is a mistake to attempt to obtain absolute population numbers by counting from a helicopter where it cannot be demonstrated that the flight response of horses is negligible. Absolute counts require low flying and intensive coverage of the landscape that are more likely to cause horse flight and, therefore, double counting. We therefore recommend cautionary investigations of the influence of aircraft on horse behaviour during population estimates. Moreover, absolute counts do not provide measures of estimate variation and statistical confidence that can be compared between and within counts to assess their accuracy and precision. We therefore suggest that managers use more rigorous techniques than simple absolute counts such as line transect (Buckland *et al.* 1993; e.g. Hone 1988), mark-resight (Pollock 1991; e.g. Caughley & Grice 1982, Bowden & Kufeld 1995) or dung density, deposition and decay sampling (Barnes 1993; e.g. Barnes & Jensen 1987) techniques. Population estimates using mark-resight and line-transect methods could be conducted from the ground or air so long as investigations of horse behaviour during estimate events suggest that the vehicles used do not confound count accuracy (see Chapter 3).

2. Assessment of the historical sequence of counts for estimating population growth

2.1 INTRODUCTION

The management of feral horse populations, particularly for the conservation of rangelands and botancial bio-diversity, has been the subject of scientific and public debate (Wright 1989; Coddington 1991; Symanski 1996; Rinick 1998). The level of population control required is influenced by estimates of population growth rates and so these have stimulated much of the debate (Cook 1975; Conley 1979; Eberhardt *et al.* 1982; Wolfe 1986; Wolfe *et al.* 1989; Garrott & Taylor 1990; Garrott *et al.* 1991a,b). The majority of reports are of populations that had high growth rates (Table 3). Such populations are more likely to pose management problems whereas stable populations pose fewer management problems and thus received less attention (e.g. Eberhardt *et al.* 1982, p. 373). Several authors (e.g. Conley 1979; Frei *et al.* 1979; Wolfe 1986) criticised the suggestion that feral horse populations could increase at their biological maximum for long periods of time. The response was to publish more data from populations with high growth rates (e.g. Wolfe *et al.* 1989; Garrott & Taylor 1990; Garrott *et al.* 1991a). Therefore, the literature has less information from slower-growing populations and encourages an expectation of high growth rates that may be mistakenly generalised to other populations.

The growth rates of 'problem' feral horse populations have largely been estimated using a sequence of single aerial counts (e.g. Eberhardt *et al.* 1982; Garrott *et al.* 1991a; Rogers 1991), although the data they provide have limitations. The large number of influences on the accuracy and precision of aerial counts have been described, and the relative importance of accuracy and precision discussed, in Chapter 1. When using aerial counts to estimate population growth, estimate accuracy can be sacrificed so long as the difference between the estimate and the true value are the same for each count and the estimate has high precision. The accuracy and precision of a sequence of single aerial counts is seldom known for estimates of population growth (Harris 1986; but see Garrott & Taylor 1990; Garrott *et al.* 1991a). Population growth rates based on sequential aerial surveys suggest rates of increase between 15 and 27% per annum (Table 3). Such rates are close to, or exceed, the biological maximum for horses (Garrott *et al.* 1991a; Cameron *et al.* 2001). Pregnancy rates have been used to corroborate high population growth (e.g. Eberhardt *et al.* 1982); however, large variation in foetal and foal mortality prevent pregnancy rates from being a reliable indication of annual recruitment. More reliable estimates of population growth rate are obtained by monitoring the birth and death rates of a population. Such estimates are uncommon for populations of feral horses where their growth rates are also measured (Table 3). There are very few populations from which detailed long-term demographic data are available for the same individuals (but see Keiper & Houpt 1984; Goodloe *et al.* 2000). Where they do exist, the studies were of intensively

TABLE 3. REPORTS OF FINITE (L) OR INSTANTANEOUS (*R*) POPULATION GROWTH OF FERAL HORSE POPULATIONS IN THE LITERATURE ALONG WITH THEIR MANAGEMENT HISTORY, POPULATION SIZE, AND ADULT SEX RATIOS. LARGE REMOVALS ARE DEFINED AS THOSE IN WHICH THE POPULATION WAS REDUCED IN SIZE BY > 50%. NR = NOT REPORTED. + DENOTES A MINIMUM ESTIMATE. REPRODUCED FROM CAMERON *ET AL.* 2001.

POPULATION	DISPERSION LIMITS	Removal history	SIZE RANGE	SEX RATIO (M per 100 F)	POPN GROWTH	Method
Paisley	nr	Large	81–307	nr	$\lambda = 1.27$	Aerial counts
Riddle Mt.	nr	Large	nr	nr	$\lambda = 1.25$	Aerial counts
Beaty's Butte	nr	Large	134–391	nr	$\lambda = 1.24$	Aerial counts
Lander complex	nr	Large	nr	nr	$\lambda = 1.23$	Aerial counts
Jackies Butte	nr	Large	78–280	nr	$\lambda = 1.23$	Aerial counts
McCullough	nr	Large	121–459	nr	$\lambda = 1.22$	Aerial counts
Beaty's Butte	100% barriers	Large	142–419	nr	$r = 0.20$	Aerial counts
Monger	nr	Large	169	nr	$\lambda = 1.21$	Aerial counts
Granite Range	None	Cattle removed	58–149	76	$r = 0.188$	Marked popn
Jackies Butte	100% fenced	Large	94–280	nr	$r = 0.18$	Aerial counts
Goshute	nr	Large	nr	nr	$\lambda = 1.19$	Aerial counts
Cold Springs	nr	Large	nr	nr	$\lambda = 1.18$	Aerial counts
Kaimanawa Mt.	partially fenced	None	174–1102	nr	$r = 0.167$	Aerial counts
15 Mile	nr	Large	94–429	nr	$\lambda = 1.17$	Aerial counts
Stockade	nr	Large	74	nr	$\lambda = 1.16$	Aerial counts
Challis	nr	Large	223–650	nr	$\lambda = 1.15$	Aerial counts
Pryor Mt.	100% fenced	Small	86–181	52	$\lambda = 1.12$*	Marked popn
Kaimanawa Mt.	none	Small localised	413	92	$\lambda = 1.096$	Marked popn
Cumberland Is.	Island limited	None since 1972	186–220+	125	$\lambda = 1.043$	Ground count

* Garrot & Taylor (1990) report an average finite rate of increase of 1.18 for an 11-year period. However, they excluded a year (i.e. 1978) within the sequence mortality such that $\lambda = 0.593$. Including this year results in an estimate of average finite population growth of 1.12 that is perhaps more representative of wha given the occasional severe winter.

managed, small or confined populations and not from populations around which the public debate is most centred (i.e. Symanski 1996, but see Berger 1986).

2.2 HISTORICAL DATA

The sequence of counts used to estimate Kaimanawa feral horse population growth did not consistently use the same method but gradually become more thorough. Kaimanawa wild horse population size was first estimated by a team of four people on foot who conducted an unstructured count of a relatively small area (Aitken *et al.* 1979) and relied on New Zealand Army estimates from adjacent regions. In 1986 the first aerial counts were conducted and later described as 'Exhaustive searches of all catchments' and 'A thorough search of 85% of the horse range' (DOC 1995). Other than these descriptions the methodology or extent of the counts are not reported. Counts like these were conducted in 1986, 1987, 1988, 1990 and 1992 (Fig. 1). The first five counts were used to construct an exponential curve and suggest that the population's average instantaneous rate of increase (r) was 0.167 (1979–90) and 0.20 in some years (1988–90: Rogers 1991, fig. 1). Rogers (1991, fig. 1) presents a confidence interval around the population growth, but it was derived from the sequence of counts and the assumption of exponential growth rather than from measured variation within individual counts. Thus, the confidence interval is not a measure of count accuracy or precision. Later, it was suggested that the population might grow by as much as 24% per year (DOC 1995). Still more methodical helicopter techniques were introduced in 1994 that utilised GPS to guide the helicopter along a sequence of adjacent flight paths that were 300 or 500 metres apart (described in Chapter 1). Thus, factors that are known to influence the accuracy of aerial counts, such as count technique (Caughley 1974; Frei *et al.* 1979; Kufeld *et al.* 1980; Gasaway *et al.* 1985; Bleich *et al.* 1990; Bodie *et al.* 1995; present study, Chapter 1), varied in different counts, as did the size of the area searched and search effort. Rogers (1991) suggested that

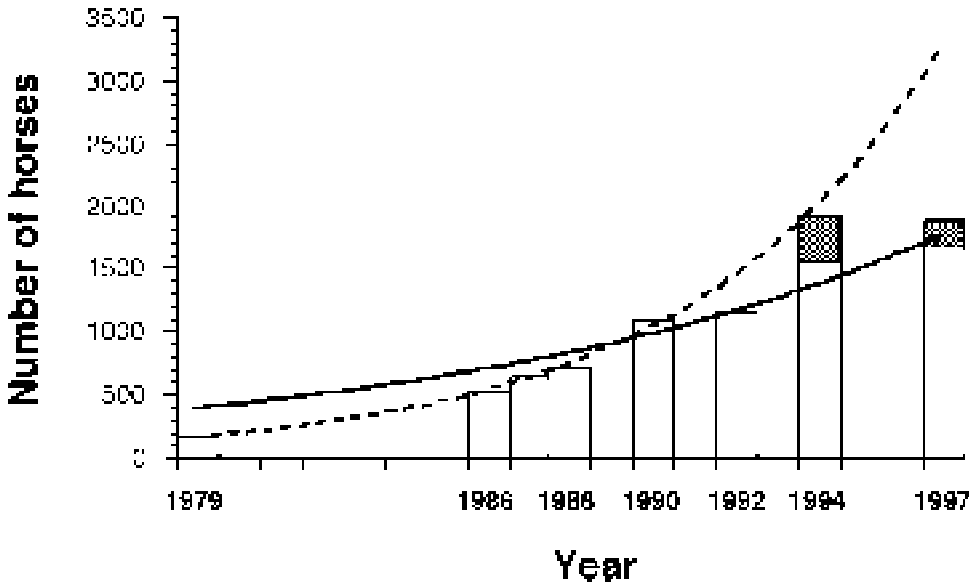


Figure 1. History of Kaimanawa feral horse population counts and projections of population growth. White bars show the number of horses counted and grey bars the number of horses removed from the population prior to each count. The dashed line shows the projected population size using Roger's (1991) estimate of population growth (r = 0.167) based on the first five counts. The solid line shows projections of population size backwards and forwards in time using our estimate of population growth (9.6% per annum) based on average estimates of age specific fecundity and mortality from 1994 to 1998 and anchored at 87% of the 1994 helicopter count.

aerial counts probably underestimated feral horse population size by 10 to 20%, but this assumption has not been tested. We have shown how a count in 1996 over-estimated population size due to the flight response of horses that resulted more horses being counted twice than were missed by observers (Chapter 1). Thus, with each aerial count DOC has invested greater effort and experience in counting horses than in the last.

2.3 POPULATION GROWTH ESTIMATE COMPARISONS

Cameron *et al.* (2001) described how detailed measures of fecundity and survivorship from 1994 to 1998 were used to estimate population growth. Their estimate of Kaimanawa average finite population growth (λ = 1.096) was around 50% lower than previous estimates based on sequential counts in the Kaimanawa Ranges (λ = 1.182, r = 0.167: Rogers 1991) and from some North American populations (e.g. r = 0.18 – 0.20: Eberhardt *et al.* 1982; λ = 1.15 – 1.27: Garrott *et al.* 1991a) but still higher than others (e.g. λ = 1.030 – 1.068, Goodloe *et al.* 2000). Cameron *et al.* (2001) considered why the Kaimanawa population growth rate was lower than most North American populations. The difference is attributable to large removal histories and artificially female-biased adult sex ratios in North American populations that have not been a feature of the Kaimanawa population. Here we consider why our growth estimates deviate from previous estimates from the Kaimanawa population (Rogers 1991; DOC 1995).

We propose that Kaimanawa horse population growth rates were over-estimated when derived by interpolating from the available history of counts because of sequential improvements in count technique and increases in count effort. Four pieces of evidence support our hypothesis:

i. estimates of the maximum possible annual rate of increase for feral horses
ii. comparisons of annual reproduction (i.e. juvenile: adult ratios) with the growth rate from the same aerial counts
iii. recent DOC aerial counts that were consistent in technique
iv. the use of our population growth rate to construct an alternative population history that can be compared with the history of Kaimanawa horse counts.

We consider each in detail below:

i. Using extreme figures of fecundity and survivorship we estimated that the maximum rate for feral horse population growth was 21.7% per annum (see Cameron *et al.* 2001). This biological maximum for feral horse population growth is similar to the biological maximum suggested by Conley (1979: λ = 1.20). Clearly, annual rates of increase up to 24% per annum (DOC 1995) in the Kaimanawa population are improbable.
ii. If there is no mortality then the foal : adult ratio will approximate the instantaneous rate of increase (r). Rates of annual reproduction in the Kaimanawa population (i.e., ratio of foals to adults from ground survey = 0.12 in 1979: Aitken *et al.* 1979; ratio of juveniles to adults from aerial counts (potential overestimate due to possible inclusion of some yearlings with the foals) = 0.14

in 1986, 0.18 in 1987, 0.19 in 1988, 0.19 in 1990: Rogers 1991) are smaller (1979–90 average ± SE = 0.164 ± 0.01) than projected rates of increase from the same sequence of counts (i.e., r = 0.167 in 1979–90: Rogers 1991) and considerably less than the upper limits of population growth proposed (i.e. 24% per annum or r = 0.215: DOC 1995). Rogers (1991) even suggested an instantaneous population growth rate (r) of 0.20 from 1988 to 1990 when his own data show juvenile : adult ratios in 1988 and 1990 were 0.19. Where the foal : adult ratio in the population is consistently the same, or smaller, than r then one is forced to conclude that there is zero, or negative, mortality. Clearly, historical measures of annual reproduction and estimates of population growth, from the same aerial counts, contradict each other. Foal : adult ratios indicate that average population growth for the last 20 years must have been considerably < 18% per annum in the Kaimanawa population. If current high rates of survivorship (i.e. around 87% for foals and 95% for adults: Cameron *et al.* 2001) are also historically representative then we would expect population growth to fall around 10% per annum from 1979 to 1990 given the average foal-to-adult ratio of 0.16.

The contradiction between annual reproduction and estimates of population growth from the same aerial counts can also be illustrated by comparing Rogers' (1991) instantaneous rate of increase (r) with the finite rate of in-

TABLE 4. THEORETICAL POPULATION DURING A FULL BREEDING YEAR (FOALING AND MATING BEGINS IN SEPT.). WE USE AN ADULT MORTALITY OF 1 ADULT EVERY 2 MONTHS (I.E. 95% SURVIVORSHIP) AND A FOAL MORTALITY OF 1 FOAL EVERY 3 MONTHS (I.E. 80% SURVIVORSHIP). WE USE A FOALING RATE OF 0.40/MARE AND FOR SIMPLICITY WE ASSUME THAT ALL FOALS ARE BORN IN SEPTEMBER AT THE BEGINNING OF THE SEASON. THESE FIGURES OF FECUNDITY AND MORTALITY ARE SIMILAR TO THOSE MEASURED DURING THE STUDY (SEE CAMERON *ET AL.* 2001). THE ACTUAL FINITE RATE OF INCREASE (λ) = N_{t+1}/N_t = 111/100 = 1.11. HOWEVER, USING ESTIMATES OF N_{t+1} AND N_t FROM COUNTS GIVES OVER-ESTIMATES BECAUSE IT DOES NOT INCORPORATE ANIMALS THAT HAVE DIED OR WILL DIE BEFORE THE END OF THE BREEDING SEASON. NOTE HOW THE TIMING OF THE COUNT RELATIVE TO THE PEAK FOALING TIME INFLUENCES THE ESTIMATE OF λ. THE LONGER SINCE THE END OF FOALING THAT A COUNT IS CONDUCTED, THE CLOSER IS THE ESTIMATE OF λ TO THE TRUE VALUE, ALTHOUGH IT IS STILL OVER-ESTIMATED BY A SIZABLE AMOUNT. ROGERS' (1991) 4 COUNTS WERE CONDUCTED AT DIFFERENT TIMES OF THE YEAR: DECEMBER, APRIL AND JULY AND THESE TIMINGS ARE ILLUSTRATED BELOW.

MONTH	ADULT POPN (est. of N_t)	FOAL POPULATION	TOTAL COUNT (est. of N_{t+1})	EST. OF λ FROM COUNT
Sep	100	20	120	1.200
Oct	100	19		
Nov	99	19		
Dec	99	19	118	1.192
Jan	98	18		
Feb	98	18		
Mar	97	18		
Apr	97	17	114	1.175
May	96	17		
Jun	96	17		
Jul	95	16	111	1.168
Aug	95	16		

crease (λ) that can be estimated from each counts using the numbers of juveniles and adults. We use the following analogous equations for the relationship between λ and r: $r = \ln(\lambda)$ and $\lambda = e^r$. We use N_{t+1}/N_t as an estimate of λ. We use the number of adults in each count as an estimate of N_t and the total count as an estimate of N_{t+1}.

Estimates of λ using these figures assume that there has been no mortality in the adult population that produced the annual cohort of juveniles in the current breeding year and that juvenile and adult mortality rates are not different. However, there will be adult mortality and juvenile mortality rates that are higher than adult mortality rates (Cameron *et al.* 2001). Therefore estimates of λ using counts of adults and juveniles will be much larger than actual values and thus over-estimate annual reproduction. The effect of these assumptions and the timing of the aerial count relative to the breeding season are illustrated in Table 4 using a theoretical population of 100 horses that produces 20 foals. The table shows how counts of the numbers of juveniles and adults to estimate N_t and N_{t+1} will over-estimate λ. Thus, our calculations of λ provide a figure higher than the true value and so our estimates are prefixed with a less-than (<) sign (Table 5). Comparisons show that there are not enough juveniles counted in the population on each count to account for the instantaneous rate

TABLE 5. COMPARISONS BETWEEN INSTANTANEOUS RATES OF POPULATION GROWTH (r) DERIVED BY INTERPOLATION BETWEEN THE SEQUENCE OF AERIAL COUNTS (1979–90) WITH ESTIMATES OF ANNUAL REPRODUCTION FROM JUVENILE AND ADULT NUMBER FROM THE SAME COUNTS. POPULATION COUNTS FROM WHICH ESTIMATES OF N_{t+1} AND N_t WERE DERIVED TO ESTIMATE λ AND r ARE SHOWN IN BOLD TYPE. ESTIMATES OF r FROM WHICH λ WAS ESTIMATED AND VICE VERSA ARE IN BOLD TYPE.

SOURCE	YEAR	EST. N_t	EST. N_{t+1}	λ	% ANNUAL REPRODUCTION	r
Individual counts						
	1979	**43**‡	**48**‡	< 1.116	< 11.6	< 0.109
	1986	**467***	**532***	< 1.139	< 13.9	< 0.130
	1987	**562***	**662***	< 1.178	< 17.8	< 0.164
	1988	**643***	**763***	< 1.187	< 18.7	< 0.171
	1990	**928***	**1102***	< 1.188	< 18.8	< 0.172
Average of counts [check]						
	1979–90			< 1.160	< 16.0	< 0.148
Interpolation from sequential counts [check]						
	1979–90			1.182	18.2	**0.167***
	1988–90			1.221	22.1	**0.200***
Upper limit guestimate						
				1.240	**24.0**†	0.215

‡ Sourced from Aitken et al. (1979, table 1) * Sourced from Rogers (1991, table 1).

† Sourced from DOC (1995). The number of adults is used to estimate N_t and the total population countedis used to estimate N_{t+1}. Where estimates of N_t and N_{t+1} are obtained this way from the same count then N_{t+1}/N_t will underestimate ? and, therefore, r. This is because they assume that there has been no mortality in the adult population in the current breeding year and that juvenile and adult Survival rates are not different. However there will have been adult mortality, and juvenile mortality occurs at a higher rate than adult mortality. Rogers (1991) estimates of r (i.e. 0.167 from 1979 to 1990 and 0.2 from 1988 to 1990) are higher than annual reproduction would allow (i.e. <0.148 1979–90 and 0.172 1988–90).

of increase that was arrived at by interpolating between the individual counts (1979 to 1990, Table 5). It is not possible for the annual increase in population size to exceed annual reproduction.

These comparisons demonstrate that either:

a. annual reproduction was consistently under-estimated in all previous studies of the Kaimanawa population (Aitken *et al.* 1979; Rogers 1991; Franklin 1995; Cameron *et al.* 2001), or

b. instantaneous growth rates, calculated by interpolating between aerial counts, are over-estimated.

We think it more likely that juvenile numbers from aerial counts over-estimate, rather than under-estimate, annual reproduction because they may include some late foals from the previous season as well as the current years foals in the count of juveniles. This leads us to be concerned about the reliability of the historical record of aerial counts to estimate population growth.

iii. Consecutive aerial counts are only useful for estimating population growth if the bias is the same size and direction across each estimate or measurable with each count (Wolfe 1986; Garrott *et al.* 1991a). Attempts by the DOC to standardise aerial counts resulted in two similarly conducted counts in 1994 and 1997 that counted 1576 and 1697 horses, respectively. These figures indicate a 10.8% annual growth rate between 1994 and 1997 (allowing for the 268 and 69 horses removed by muster between counts in May–June 1994 and 1995, respectively) that is considerably less than previous estimates and similar to ours (see also Cameron *et al*. 2001). Consequently, contemporary standardised aerial counts support our figures of population growth during the same period.

iv. It is not possible to assess exactly how much of the measured population increase as judged from historical counts was due purely to changes to counting methodology and effort and how much to a real population increase. Nevertheless, if we assume that current low rates of mortality (i.e. Cameron *et al.* 2001) are historically representative, the consistency in the foal (or juvenile): adult ratios observed from 1986 to 1997 suggests that our estimate of population growth rate from 1994 to 1997 may be representative of population growth over the last 20 years. In addition, we showed that contemporary helicopter counts over-estimated population size over 176 km^2 of the range by around 13% (Chapter 1). Thus, if we find 87% of the 1994 aerial count (helicopter count minus a 13% over-estimate) and use our estimate of population growth rate to extrapolate backwards and forwards in time, we construct an alternative Kaimanawa horse population size history (Fig. 1). As expected from our assessment of previous counts, the proposed history suggests that early counts underestimated population size but that the amount of under-estimation declined as more effort was invested in counts and counting technique improved until current methods were introduced that extended the trend towards population size over-estimation. Note that our projected population size for 1997, from 1994 based on a population growth rate of 9.6% per annum, almost exactly matches the actual population size (based on the aerial count minus 13% over-estimate) whereas Rogers' (1991) projected population growth was not predictive (Fig. 1).

We hope that this new information encourages scepticism of count data suggesting that the average growth of the Kaimanawa population was 18.2% per annum for a 12-year period (i.e. $r = 0.167$: Rogers 1991) and discourages further claims that it may increase at rates up to 24% per annum (DOC 1995). The interpolation between inconsistent counts of Kaimanawa wild horses in New Zealand has exaggerated the population's growth rate. Reports continue to appear implying that variable counts from 1979 to 1994 can be reliably used to estimate population growth (e.g. Fleury 2000).

Doing so implies:

a. contradicting annual recruitment data from all surveys (point ii above) that suggest a lower growth rate
b. ignoring the changes in count technique and effort that are known to influence count accuracy
c. having faith in the accuracy of the unstructured and incomplete ground count in 1979.

We recommend caution in the use of historical counts to estimate population growth rates where it cannot be shown that count methods were the same and consistently applied. We encourage greater reliance on studies that provide direct and concurrent measures of fecundity and mortality and estimates of their annual variation (e.g. Keiper & Houpt 1984; Berger 1986; Siniff *et al.* 1986; Goodloe *et al.* 2000) to support estimates of population growth. A fortuitous history of single counts and retrospective checks of their reliability are not a substitute for more rigorous demographic studies. We commend recent attempts by DOC to standardise helicopter count techniques (DOC 1995) to allow more precise estimates of population change. However, we caution that while the real accuracy and precision of counts remains unknown the reliability and sensitivity of helicopter counts for estimating population growth will continue to be in doubt and contestable. Estimates of population growth would be more convincing if the current helicopter counting method was replaced by two other methods that sample, rather than attempt to census, the population. The recent removal of most of the population and it restriction to a smaller part of the range that was the focus of detailed study (i.e. Cameron *et al.* 2001), provide the opportunity to apply better methods of population monitoring. Alternative methods are trialed and discussed in the following chapter.

3. Trialing other population monitoring methods

3.1 INTRODUCTION

In most circumstances it is impossible to census wild ungulate populations. There are too many influences on census accuracy and precision that we have described in Chapters 1 and 2. More importantly, census methods like the helicopter counts conducted by DOC (i.e. a sequence of single attempts at complete counts over 15 years), do not quantify sources of variation within and between counts. Thus, judging the reliability of a count or the difference between two or more counts over a period of years is not possible. Estimates of population size and change are more convincing if the accuracy and precision of individual population estimates is quantified. It is for this reason that sampling to estimate population size is preferable to census methods. Sampling methods provide statistical measures of variation and intervals of confidence for the estimates of population size and growth. Therefore, we have recommended that if helicopter counts are retained then their accuracy and precision should be quantified and that a second independent population monitoring method be instituted to support its results. Alternatively, managers could replace helicopter counts with two or more population sampling methods to monitor population size and growth. In this section we describe the trial of three sampling methods of population size monitoring in the Southern Kaimanawa Ranges: line-transect distance sampling, mark-resight sampling and dung pile density, deposition and decay sampling. We discuss the advantages and limitations of each technique for monitoring the current reduced population of Kaimanawa horses.

3.2 METHODS & RESULTS

Line-transect distance sampling

Line transects that could be negotiated on a four-wheel drive all-terrain vehicle (A.T.V.) were established through each zone (see Cameron *et al.* 2001, chapter 3, fig. 3). Observations along four line transects in the Waitangi (W), three in the Hautapu (H) and three in the Southern Moawhango (SM) zone were conducted in April (mid autumn) and October (mid spring) 1995. In the Southern Moawhango zone, additional observations along line transects were conducted in January (mid summer) and July (mid winter) 1995. The line transects ranged in length from 8.0 to 18.9 km from one side of a zone to the other. Line transects were conducted between 0800 and 1600 hours NZST when visibility was good. Adjacent transects were not conducted on consecutive days to minimise the impact of conducting one transect on the results of the other. Speed of travel along line transects was limited by rough terrain but confined to below 15 km/h where transects followed formed roads or tracks. One line transect in the Waitangi zone could not be negotiated on an A.T.V. and was conducted on foot.

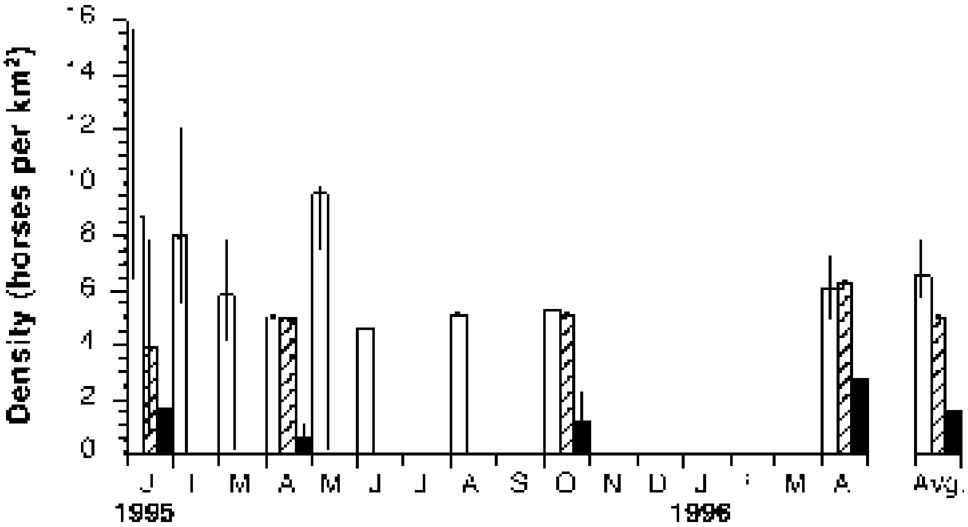


Figure 2. Density of horses in the Southern Moawhango (white), Hautapu (///) and Waitangi (black) zones (vertical lines indicate 95% confidence intervals from Bootstrap analyses (n = 1000) of density estimates using DISTANCE) from line-transects. The average density of each zone (Avg.) is calculated by using each sample occasion from January 1995 to April 1996 as a replicate and bootstrapping as above (reproduced from Cameron *et al.* 2001).

The locations of horse groups sighted from the line transect with the naked eye were recorded to the nearest 10 metres on 1 : 25 000 scale topographical and vegetation maps, and the size, age class (foal, yearling, sub-adult and adult), sex and distinguishing features of individuals within each group recorded. Detailed observations of bands and individual horses were made using telescopes (15–60×) and binoculars (10–15×) where necessary. Descriptions of individuals and groups were used to prevent duplicating observations of horses along transects. The perpendicular distance between each horse group and the line transect was determined by measuring the distance between the group's location as marked on the map and the line transect and ranged up to 2.7 kilometres.

The perpendicular distances and group sizes were entered into DISTANCE line-transect software to estimate horse density (Buckland *et al.* 1993; Laake *et al.* 1994). Estimates of density were calculated for each zone by pooling transects contained within each and stratifying by month. Estimates of density for the entire Auahitotara ecological sector were stratified by zone and by month. The Fourier series with truncation where $g(x)$=0.15 and grouping of the perpendicular measures into even intervals (SM n = 4, H n = 7, W n = 10) were used to construct the detection functions for the transects in each zone. The best number of even intervals for grouping of perpendicular distances, and level of truncation, were determined retrospectively to minimize the estimate's co-efficient of variation and remove distance clumping effects. The estimation process checked for a relationship between group size and visibility from the line transect. Significant relationships were not found and so average group size was used to estimate density from the number of groups and their distance from the line transect. In this way population size estimates and their 95% confidence intervals were calculated using 1000 bootstraps of the density estimation process (Buckland *et al.* 1993; Laake *et al.* 1994).

In the Auahitotara ecological sector the density (and the 95% confidence interval of the density estimate) of horses was 2.8 (1.9–4.0) and 3.6 (2.8–5.4) horses/km^2 in April and October 1995, respectively. Densities in the Southern Moawhango, Hautapu and Waitangi zones were 5.2 (3.6–8.9), 5.0 (2.6–7.6) and

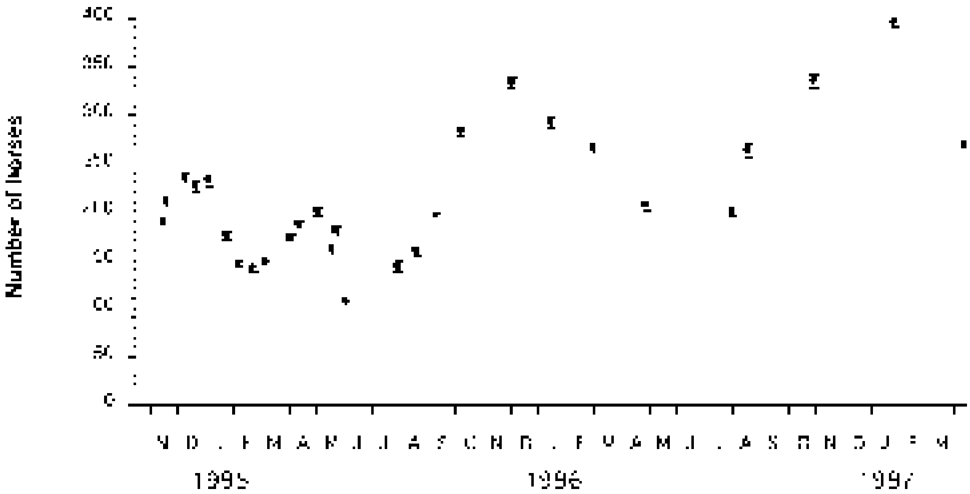


Figure 3. Population estimates of the number of horses in the Argo Basin (error bars show 95% confidence intervals of the estimate) from November 1994 to March 1997. Note the season cycle in the number of horses in the Argo Basin that results in largest numbers being present from late spring to the end of summer each year, due to seasonal changes in habitat and home range use (reproduced from Cameron *et al.* 2001, see Section 4.6 for discussion of the reasons for this annual cycle).

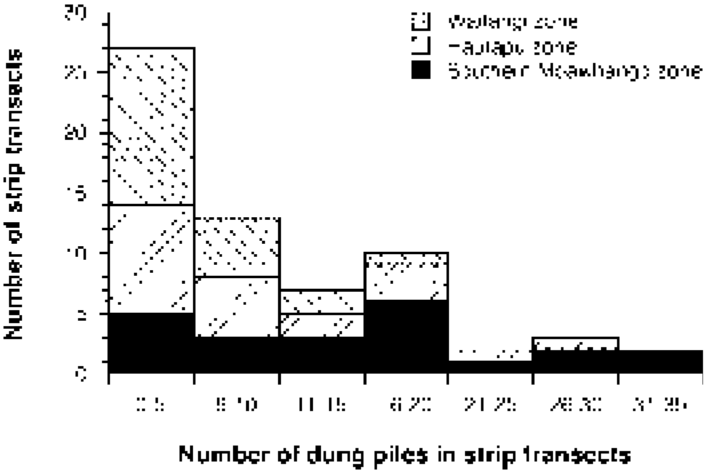
0.9 horses/km^2 (0.5–1.5), respectively, as calculated from April and October 1995 line transects (Fig. 2). The number of horse groups sighted from individual line transect was not always enough (i.e. sometimes < 20 groups) to reliably estimate of population density. Better estimates were obtained by pooling the result from three or four transects within each zone. However, estimates from the line transects within each zone on single occasions still produced highly variable results with large 95% confidence intervals (Fig. 2). The precision of line-transect result was improved by replicating the same line transects in different months or seasons and using each occasion as a replicate (Avg. bars in Fig. 2). Data were then entered into DISTANCE stratified by occasion as well as region to obtain an estimate that uses the different occasions as replicate estimatess of population size.

Mark-resight sampling

A sub-population was captured by mustering from the Argo Basin in June 1994. Each captured horse was branded with two 2" × 3" freeze brands on their right rumps to provide an individual mark. Resight events were conducted when visibility was not impeded by weather and there was no other human activity in the area; they took between 5 and 9 hours to complete. During resight events two observers each walked an approximately circular route through the northern and southern halves of the Argo Basin recording the size and composition of all groups of horses. Population estimates for the Argo Basin were calculated from estimates of the numbers of bands, obtained by using NORMARK mark-resight software (White 1996), and average band size.

The number of horses in the Argo Basin showed a seasonal cycle with more horses present in the summer than in the winter (Fig. 3, see Section 4.2 of Cameron *et al.* 2001, for discussion of the causes of this annual cycle). Estimates using mark-resight methods had high precision due, primarily, to the large proportion of the population being marked and resighted (i.e. 65 to 90% of groups resighted were marked). The precision of estimates will deteriorate as the proportion of the population that is marked declines.

Figure 4. Frequency distribution of dung piles in the 64 strip transects (3 m × 100 m) conducted in the three zones.

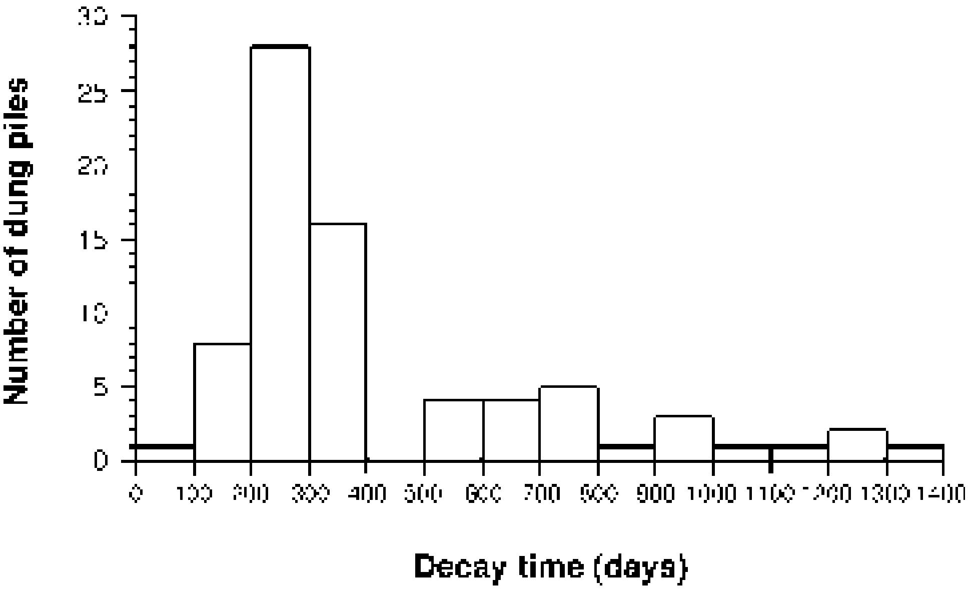


Dung sampling

Dung density

The 11 line transects used for distance sampling were also used to measure dung density in April–May 1996. We traveled to restricted random points along each line transect that provided on average one sample point every 1 kilometre. From this point we walked a random number of paces (<1000) to the left or right and perpendicular to the line transect. At the arrived point we laid out a 100-metre tape approximately parallel to the line transect. Using a metre rule we counted all adult (foal dung piles can be differentiated by their size, *pers. obs.*) dung piles within 1.5 metres of the tape. In this way we randomly counted the number of dung piles within 64 × 300 m^2 randomly located strip transects within the Auahitotara ecological sector. The number of dung piles in strip transects ranged widely within and between zones as expected from our previous observation that the density of horses differs between zones and that horses are selective of habitat (Fig 4).

Figure 5. Frequency distribution of decay by dung piles.



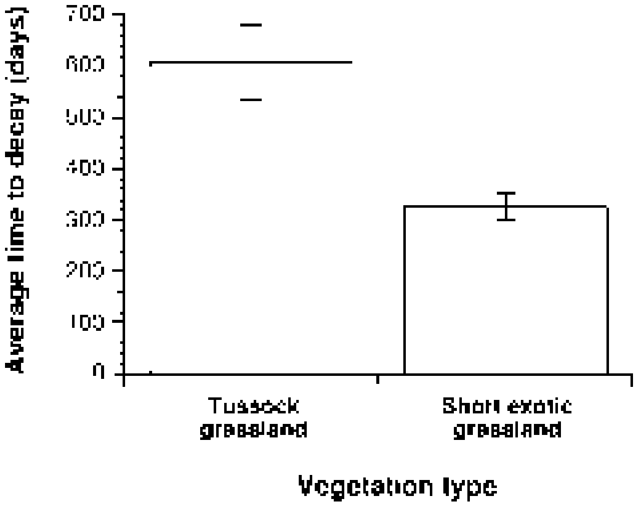


Figure 6 (Above). Difference in dung decay time in tussock compared with short-exotic grasslands.

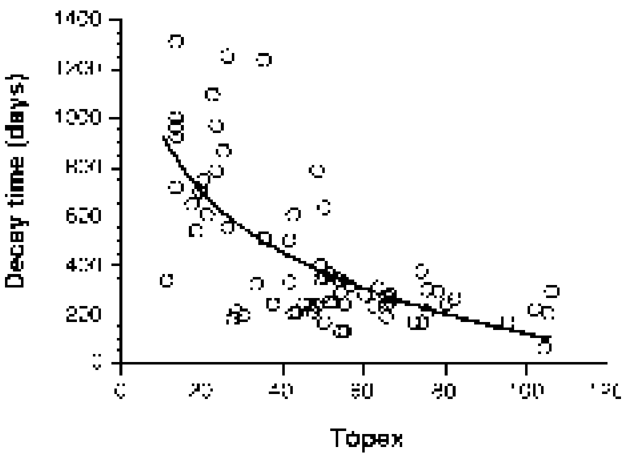
Dung deposition rates

We sampled dung deposition rates by observing focal bands for 1 to 2.5 hours to obtain 370 hours of observation of individual horses. During this time 123 defecation events that resulted in a dung pile were observed. Thus, horses deposited 0.351 ± 0.037 (SE; range 0–0.882) dung piles per hour or one dung pile every 2.85 hours.

Dung decay rates

The Argo Road runs through the centre of the study area and the Southern Moawhango zone and passes through all habitat, vegetation and topography types in the region (Cameron *et al.* 2001: fig. 3). When adult (>1-year-old) horses were observed to defecate in the vicinity of the Argo Road, the dung pile was marked with a permanent wooden peg and given a unique identity number and the date of deposition noted. Whether the dung was deposited in tussock or exotic grasslands was noted, if appropriate, and the topex of the site measured. Topex is a relative measure of a site's topographical exposure that is used traditionally by foresters to measure the suitability of a site for planting trees (Tombleson 1982). It is derived from the sum of angles to the horizon at the eight cardinal compass points. We measured these using a compass and Abney level. High and low topex scores indicate that a site is sheltered and exposed, respectively. In this way we marked and described the environment of 80 dung piles from May 1995 until March 1997 along the Argo Road from where it enters the Argo Basin at 700 m a.s.l. to where it leaves the Southern Moawhango zone at the height of the Westlawn Plateau (1240 m a.s.l.). We visited the dung piles every month to record whether or not they were still visible when standing within 1.5 meters of the pile (half of the width of strip transect for counting dung, see above). We determined the date of dung pile disappearance as the mid-point between the date of the visit when last visible and the visit date when no longer visible. The time to dung disappearance was the number of days between this date and the date when the pile was first deposited.

Figure 7 (Below). Relationship between dung decay time and the topex of the site at which the dung was deposited. Topex is a measure of topographical shelter. Where topex is high the site was more sheltered. The line of best fit through the data points is described by the equation: decay time = 1786 – 835.41 log (topex) (R = 0.70).



The rate of dung pile decay varied tremendously (Fig. 5). Most dung piles disappeared before just over a year had elapsed but others lasted longer than 3 years. The large variation in the rate of dung decay indicates that the habitat in which a dung pile is deposited dictates the rate of decay. For example, we found that dung piles in open exotic grassland decayed at a faster rate than those in tussock grasslands (Fig. 6). Dung piles in sheltered sites (that is with a high topex score) decayed at a faster rate than those in exposed sites (Fig. 7). The average rate (± SE) of dung decay was 424 ± 34 days.

Estimating population density from dung density, decay and deposition

The average density of dung in the three zones of the Auahitotara ecological sector was 494 (SM), 279 (H), and 159 (W) piles per hectare. Using the average rate of dung decay and deposition it is possible to calculate the average density of horses in the zone during the period before the present that it takes dung to decay (i.e. 1 to 4 years) in the following way:

[Dung density (dung per hectare)/ Dung deposition rate (dung per horse per hour)]/ Dung decay time (hours).

For example:

Where strip transects show an average dung pile density of 497 per hectare (i.e. 14.9 per 300 m^2 strip transect), an average dung deposition rate of 0.351 per hour, and an average decay time of 424 days (10176 hours) then the estimated density of horses is (497/0.351)/10176 = 0.139 horses per hectare or 13.9 per km^2.

Using average figures of dung density, deposition and decay from the three zones we thus calculate an average density of 13.9, 7.8 and 4.4 horses per km^2 in the SM, H, and W zones respectively for the 3–4 year period to April 1996.

3.3 DISCUSSION

The trials of line-transect, mark-resight and dung density sampling illustrate that population size can be estimated successfully in other ways that provide measures of estimate variation and confidence that are not provided by current helicopter counting methods. This is particularly true now that the population has been substantially reduced and ranges over a smaller area that includes the region and population intensively studied (Cameron *et al*. 2001). The trials on this population helped to identify the advantages and limitations of each technique and ways that each might be better applied.

Line-transect sampling

Line-transect estimates assume that:

a. no group is recorded more than once per transect
b. groups do not move in response to the observer prior to being sighted and their position determined
c. the probability of a group being sighted on the line transect is 1.0
d. that line transects are randomly placed.

Whenever a group was sighted its size, composition (age class as foal, yearling, sub-adult, adult and sex by external genitalia), and the distinguishing features of its individuals were recorded using telescopes (15–60×) and binoculars (10–15×) and used to prevent duplicating observations of the same horses along each transect. The first assumption is most likely to be violated if horses move in response to the observer or line transects provide different views of the same area at different places along the transect. Ideally line transects will be near-straight lines of travel and horses will not move in response to the observer. With an observer on a motorbike or walking, no groups were observed to walk towards the observer out of curiosity during transects. Moreover, only 19 of 558 horse groups were walking away from the observer when first sighted and none were observed at faster gaits (Linklater *et al.* 2000b). Thus, the movement of groups in response to the observer was negligible but might be more serious for aircraft (see Chapter 1). The probability of detection was greatest on the line transect and declined or was constant with increasing distance from it for all detection functions constructed by the density estimation process. It is unlikely that an approaching observer would not see a group of horses that straddled the line transect since the grass- and shrub-land vegetation of the range is not tall enough to obscure horses. This is particularly true because horses live in groups and tend to leave cover and stand together when they become aware of an observer. Therefore, the first three assumptions of the line-transect method were satisfied and are relatively easy to satisfy during ground-based line transects. The final assumption was not satisfied in the trial described. Line transects could only be placed through habitat that can be negotiated on a motorised vehicle, in this case a 4-wheel drive motorbike. Negotiable habitat is more likely to be short grassland and gentler slopes. Both of these two habitat characteristics are strongly selected by horses (see Cameron *et al.* 2001). Thus, line transects conducted in the way described are likely to over-estimate population size because horses are more likely to be found on, or closer to, the line transects than if transects were randomly placed. The problem of line-transect placement could be overcome by conducting line transects from the air. However, observers would need to be certain that the aircraft did not influence horse behaviour such that the other assumptions of the method were violated. Our observations of horse behaviour in response to a helicopter (Chapter 1) suggest that aerial line transects are likely to violate the assumptions of the method. Alternatively line transects could be conducted on foot. The quieter and slower travel on foot meant that horses were not disturbed by the observer prior to them being sighted and counted. Multiple line transects across the horse range by different observers could be conducted on the same day. Line transects could be randomly defined and observers, guided by compass, dropped at the line-transects origin and picked up again at the other side of the range. Line-transect spacing would be restricted to distances greater than the maximum visibility from the line transect. Measuring the distance of a group of horses from the line transect (or observer where the angle from the transect line will also need to be estimated) will be more difficult where observers are not familiar with the region and may require the use of range-finders, or binoculars and field telescopes with eye-piece micrometers.

Mark-resight sampling

The location of marked breeding groups inside or outside the mark-resight area was known due to 20 regular band relocation events every 9 days (average, range 3–21 days) from November 1994 until March 1997: Linklater 1998). Therefore, closed population mark-resight techniques could be used. However, where less intensive observations mean this knowledge is unavailable, open-population techniques could be used. Mark-resight estimates assume that:

a. all groups had the same probability of being marked

b. the marking of groups does not affect their re-sightability

c. all marked groups were correctly identified

The freeze-branded individuals were gathered for marking by helicopter muster in June 1994. Other helicopter musters of the Argo Basin in 1995 gathered more than 80% of resident groups and individuals returned to groups and historical home ranges after release (pers. obs.). The remainder of marked groups were 'marked' by description of the unique features of their individuals. Thus, approximately 90% of groups in the resight area had marked members and provided high marked : unmarked ratios in resight events. Freeze brands were small relative to the size of the horse and did not change horse visibility but were large enough to reliably identify horses from a distance. The resight event was a visual search of the Argo Basin following a circular route. It was possible to view the entire resight area from various vantages included in the mark-resight route. Thus, all groups were identified using binoculars or telescopes, and, if necessary, by approaching them. Approach was possible because they were habituated to the close proximity of observers (e.g. Cameron & Linklater 2000; Linklater & Cameron 2000). Therefore, these assumptions of the mark-resight method were satisfied in the current trial. Unfortunately, the detailed monitoring of bands that occurred during this trial will not always be possible and so the assumptions of mark-resight methods will not always be so easy to satisfy. In particular, the large proportion of marked groups and high marked : unmarked group ratios during resight events recorded here will only be possible in future studies if there are regular muster-mark-release events that capture a large proportion of the population. The non-random capture and marking of horses by muster will more likely violate the assumption of random marking where a smaller proportion of the population is marked, and where unmarked bands cannot be marked by describing their natural markings to compensate for muster bias. Nevertheless, where the population is maintained at around 500 horses in a smaller region, and managed by regular muster events for removal and/or contraceptive administration (see Cameron *et al.* 2001), population monitoring using mark-resight or mark-recapture becomes feasible with minor additional effort to an existing management program. Mark-resight analyses could not only provide population size estimates but detailed demographic information for individual horses of known sex and age. This level of monitoring would make it possible for managers to detect more subtle changes in fecundity and mortality than is otherwise possible using helicopter counts, line-transect or dung density estimates of population size and distribution. Nevertheless, mark-resight sampling is likely to require greater effort and time unless it can be amalgamated into a management program that already requires the capture and handling of horses.

Dung density

Previously, dung densities have been largely used as an index of animal density (e.g. Barnes & Jensen 1987). The technique has been widely used because it is inexpensive and easy to implement in difficult and remote habitat. However, the limitations of the technique are well understood (Barnes & Jensen 1987, Barnes & Barnes 1992, Barnes 1993). In particular, there is not necessarily a simple relationship between dung and animal density. This is because of spatial and temporal variation in dung deposition and decay rates. In some habitats dung will decay faster than in others. It is even possible that in some habitats horses deposit dung at a faster rate than in others, particularly if defecation rates differ with animal activity (e.g. grazing versus travelling). Our results confirm that the density of dung alone is not a useful index of horse density since dung decay rates differed dramatically between different habitats. Thus, horse density would be over-estimated in some and underestimated in other habitats. If, however, dung deposition and decay rates are known, dung densities may be used to calculate actual animal densities (Barnes & Barnes 1992). We have gone part of the way to doing this using average estimates of dung deposition and decay rates for Kaimanawa horses. However, the technique's accuracy would be improved by having estimates of dung deposition and decay for each site at which dung density is measured, rather than applying averages to all sites.

Horse densities calculated from dung pile densities are larger than those we obtained using line-transect estimates. Dung density estimates could result in over-estimates of horses density if:

i. plots are not randomly placed such that dung density is over-estimated

ii. the rate of dung deposition by horses is under-estimated

iii. the rate of dung decay is over-estimated

Although strip transects were randomly placed along and away from line transects, the line transects were limited to habitat that was negotiable on an A.T.V. Therefore, we anticipate a small bias in dung density measures towards higher densities because horses prefer shorter vegetation and gentler slopes (Cameron *et al.* 2001). Dung deposition rates were derived from observations of horses. If observers occasionally missed defecation events, our estimate of deposition rate will be slightly lower than the true value and result in an over-estimate in population size. Furthermore, we assumed that dung deposition rates do not change with time of day. This assumption has not been tested. In particular, dung deposition rates at night, dawn and dusk may differ from those during the day. Lastly, dung piles marked to estimate decay rate were not chosen randomly in space and time but chosen so that they were spread throughout the different habitats along the Argo Road. In particular, although the Argo Basin's floor makes up a small proportion of the Southern Moawhango zone, around half of the marked dung piles were located there. The Argo Basin's floor is predominantly short exotic grasslands and is topographically sheltered (i.e. has a high topex score) such that dung decayed more quickly there (Fig. 6 and 7). Thus, we sampled dung decay disproportionately from habitats in which decay is faster and thus an average of all dung decay data over-estimates the size of the population. Therefore, there is likely to be a large bias in our dung decay observations towards dung which decayed quickly and our average dung decay rate will be less than the true value. Consequently, we expect the densities of horses derived from calculations of dung density, decay and deposition to be larger than densities measured by more direct means.

Improved accuracy from dung density will depend on randomly placed strip transects, further estimates of dung deposition rates (perhaps using penned horses monitored for 24 hours on different vegetation), and more importantly a true average dung decay rate. Even better population estimates could be arrived at if dung decay and deposition rates could be estimated for each site at which dung density was measured. The importance of easy-to-measure environmental variables like altitude, vegetation, and topographical shelter for dung decay suggests that it would be possible to construct a predictive model of dung decay rates. With such a model dung decay rates could be estimated for each site at which dung density is measured. This would remove the errors associated with averaging decay rates where they vary greatly with site.

Despite the flaws in the current analysis the results are encouraging. In particular, the estimated densities from the three zones were of the same order and differed in similar proportion to the estimates from more direct means. Clearly, the method is sensitive to spatial differences in horses density of the range observed at present in the study area (i.e. 2 to 7 horses per km^2). However, horse density estimates using dung density are unlikely to be an effective replacement for more direct means (e.g. line-transect and mark-resight techniques) since there are large uncertainties associated with the measurement of dung decay and deposition rates. Thus the technique is comparatively crude and unlikely to be sensitive enough to statistically determine small changes in population size and density with time, although it may be a useful complement to another density estimation technique such as line transects and for understanding changes in habitat use patterns with time.

Horses lend themselves to the use of this technique better than other species that produce less visible and robust dung and prefer more densely vegetated habitat that is more difficult to work in (e.g. deer and possums). However, the number of variables that must be controlled to enable the use of dung for estimating animal density is very large and requires detailed and accurate measures of the spatial and temporal variation in dung decay and deposition. Where a small (approx. 500) population is managed within a smaller range (i.e. Auahitotara ecological sector) dung pile densities, combined with revised estimates of decay and deposition rates, may be an easy-to-implement and effective technique for monitoring changes in the distribution of horses. This would particularly be the case where horses move into the surrounding areas previously cleared by muster. Deviations in dung density from zero in these areas will be relatively easy to detect with statistical significance, even with methods such as this that have low precision. Thus, dung is likely to be a useful monitoring tool for recolonisation and extra-population dispersal.

4. Conclusions

Accurate and repeatable estimates of population size, distribution and growth are necessary for the appropriate management of populations. For the management of icon species, such as wild horses, rigorous estimates of population size and change that can be defended in scientific, public and legal forums are imperative if management is to proceed with minimal hindrance (e.g. Symanski 1996). To date individual estimates of the Kaimanawa populations size, called helicopter censuses, have varied in technique, effort and the area they covered. We have first examined the current helicopter counting technique and demonstrated the confounding influence of horse flight behaviour on its accuracy and precision (Chapter 1). Second, we examined the use of the historical sequence of single counts for estimating population growth rates. We showed how estimates of annual reproduction and growth from the same counts contradict each other. Annual reproduction, estimated using juvenile : adult ratios, suggests population growth rates lower than those arrived at by interpolating between the counts from 1979 to 1990. We propose that improvements in count effort and technique probably resulted in gradual improvements in horse detection with each count and, thus, the sequence of counts over-estimated population growth (Chapter 2). Estimates of annual reproduction and high survivorship indicate population growth rates around 10% per annum. The problems of using historical counts and the effect of recent helicopter count methods on horse behaviour led us to recommend against continued use of these data and methods, and to trial alternative population monitoring techniques. Finally we described the use of line-transect, mark-resight and dung density, deposition and decay sampling as alternative, or complementary, methods of population monitoring (Chapter 3).

In his review of the draft manuscript (i.e. Cameron *et al.* 2001) R. Garrott referred to the Department of Conservation (DOC) helicopter count method and our assessment of it thus:

'*The analysis of helicopter counts is valuable. Anyone widely experienced with counting feral horses would not consider the approach used, i.e., evenly spaced transects, due to the obvious risk of moving bands into the next flight line.*'

'*I agree that the presently-used aerial line transect approach with evenly spaced lines is not appropriate for feral horse surveys. If line transects are to be used, then it likely will be necessary to select lines with repeated restricted random design so that independent samples can be used to compensate for the fact that bands are driven onto the next transect line*'.

Although Rogers (1991) and DOC (1995) have used the international scientific literature to support the DOC helicopter count method, the method used is not like that used in North America. When the international literature refers to helicopter counting it means a sampling program that employs more rigorous sampling methods such as strip- or line-transects and double count techniques (e.g. Siniff & Skoog 1964; Caughley 1974; Bayliss & Yeomans 1989; Pojar *et al.* 1995). Aerial counts in the Kaimanawa Mountains have not been aerial samples, but attempts to census the population. The accuracy and precision of this type of count for estimating population size and growth is not known.

Count methods have not been described in sufficient detail to be repeatable by independent observers. Nevertheless, we were able to assess the current methodology. We found that the 1996 aerial count overestimated population size by 13% within half of the range when compared to population estimates from line-transects and mark-resight methods. Double-counting was caused by the contagious flight behaviour of horses. During flight, horse groups changed in composition, crossed several helicopter paths, and moved into other count strata where they were re-counted. Net over-counting of marked horses corresponded to population over-estimates. Thus, the current helicopter count technique cannot be said to consistently under-estimate population size by 10–20% and it may result in small over-estimates.

The literature has so far ignored the problem posed by feral horse behavioural responses to low-flying aircraft on the population estimates using them. Although more work has been done in the U.S.A. to legitimize the aerial counting method for feral horses, differences from the true number may still be large (i.e. 41% to 112% detection: Garrott *et al.* 1991a: p. 645, table 2). The inaccuracy and low precision of other aerial counts may also result, at least in part, from increases in the rate at which horses are counted twice or not counted due to their flight behaviour. We think that there is a strong case for improvements in feral horse population estimation methods that consider the confounding influence of horse flight behaviour.

Some may regard the extent of over-estimation observed (i.e. around 13% over 176 km^2) as an acceptable error. However as yet, we do not know how consistent this pattern of over-estimation is between helicopter counts. If it is consistent then this level of inaccuracy may be acceptable because precision is high. However, the count varied widely from the true value in both directions in adjacent regions resulting in large under- and over-estimates. If this variability and level of error is also observed between counts then precision is low relative to expected annual population change (i.e. 16% under-estimate to 54% over-estimate cf. population growth of around 10% per annum). Moreover, because helicopter counts are not sampling regimes the precision of individual counts is not known, although the single DOC count-remove-recount event suggested a small under-estimate in population size by the 1997 count. The tendency to seek an absolute population number (i.e. aerial 'census') achieves, in practice, the poorest quality information that may not be accurate nor comparable with other counts or between areas of the Kaimanawa horse range.

Count methods have not been the same in different years (Table 6) but have varied in technique, observers, range coverage and effort. All these factors are known to influence the accuracy of aerial counts (Caughley 1974; Frei *et al.* 1979; Kufeld *et al.* 1980; Gasaway *et al.* 1985; Wolfe 1986; Bleich *et al.* 1990; Bodie *et al.* 1995). Consecutive counts are not useful for estimating population growth unless the bias is the same size and direction across each estimate, or is small. The bias should also be measurable and predictable. Therefore, the methodology must remain the same for all consecutive counts. Even so, consecutive counts provide less accurate rates of population increase than measuring population birth and death rates (see Cameron *et al.* 2001). Early counts probably under-estimated population size, particularly because they

TABLE 6. COUNTS CONDUCTED ON KAIMANAWA WILD HORSES USING DETAILS FROM ROGERS (1991), DOC (1995) AND CAMERON *ET AL.* (2001). QUOTES ARE FROM DOC (1995).

YEAR	COUNT	JUVENILE : ADULT RATIO	MODE	DESCRIPTION	HEIGHT	WIDTH	SPEED
1979	174	0.12	Ground	Ground search of some of the horse range (800 ha)			
1986	532	0.14	Helicopter	'Exhaustive search of all catchments'	NR	NR	NR
1987	662	0.18	Fixed wing	NR	NR	NR	NR
1988	763	0.19	Helicopter	'Exhaustive search of all catchments'	NR	NR	NR
1990	1102	0.19	Helicopter	'Exhaustive search of all catchments'	NR	NR	NR
1992	1183	NR	Helicopter	'Thorough search of 85% of the horse range'	NR	NR	NR
1994	1576	0.197	Helicopter	'Satellite navigation and transect coverage'	NR	tr-500 m count-all	NR
1996	1697	NR	Helicopter	'Satellite navigation and transect coverage'	Approx. 60 m	tr-300 m & 500 m count-all	Approx. 60 knots

NR = not reported; tr = width of flight transect; count = area within which all horses were counted; all = all horses seen counted regardless of position relative to flight path.

visually covered the range less intensively than the current GPS guided helicopter technique and did not search the whole horse range. Including the 1979 count when interpolating population growth is particularly problematic, because it was a ground-based estimate that relied on Army Training Group estimates outside the search area, whereas later counts were more extensive aerial estimates. Recent counts were more structured, thorough, and covered the entire horse range, and may overestimate population size. Therefore, when a line is drawn through a plot of these counts, its slope is likely to over-estimate population growth. It is not possible to assess how much of the measured population increase is due purely to changes to counting methodology and how much to a real population increase. This problem will continue to plague Kaimanawa feral horse monitoring programs so long as methods are not documented for reference and inconsistently applied. Therefore, counts prior to 1994 should not be used to estimate population growth rates. These will inevitably result in over-estimates of population growth. Measures of annual reproduction (i.e. juvenile or foal : adult ratio c. 0.165) from the same counts indicate the rate must have been around 10% per annum assuming current levels of survivorship (i.e. around 94% per annum, 1994–98) that are high relative to other feral horse populations. Helicopter counts since 1994 could be used so long as the method observed in 1996 (Chapter 1) is consistently applied. Counts since 1994 confirm our population growth rate estimate of around 10% per annum (Fleury 2000). Nevertheless, helicopter counting of the type observed still has serious limitations. Its accuracy is not yet known with confidence, it does not provide replication for estimates of precision, and it may create aberrant differences in population size between regions and counts due to horse flight behaviour.

That increasing effort and rigour with successive aerial counts may account for some of the other extremely high horse population growth rates reported (e.g. Eberhardt *et al.* 1982) has been extensively debated. The finite upper limits of population growth were revised downward (Wolfe 1986) but later upward again (Wolfe *et al.* 1989; Garrot & Taylor 1990; Garrott *et al.* 1991a), but not as high as earlier estimates (Cook 1975). Garrott *et al.* (1991a) concluded that aerial counts of the type conducted in North America have provided satisfactory estimates of finite population growth. This is not the case in New Zealand. Unfortunately, how aerial counts were conducted in North America is not reported in these same papers and so we cannot ascertain why the New Zealand experience is different from that in North America. Nevertheless, the New Zealand experience of aerial counts described here is an instructive reminder for prudent critique of aerial count methods and data.

The Kaimanawa horse population was reduced to near 500 horses in 1997 and the majority of the remnant population lives in the Auahitotara ecological sector. The marked focal population, mostly living in the Southern Moawhango zone (Cameron *et al.* 2001), constitutes a large proportion of the remaining population. We found the flight behaviour of horses in the Southern Moawhango zone to result in the worst disparities between helicopter count and ground-based population estimates due in part to the high density of horses there, but also possibly to their prior experience with helicopter mustering. Where the population is larger and spread across a larger range, over-counting in one area or habitat may be compensated by under-counting in another. For example, in the Auahitotara ecological sector, over-counting in the Southern Moawhango zone was to some extent compensated by under-counting in the Hautapu and Waitangi zones (Table 2). However, where the population is smaller and less widely distributed, the unpredictable influences of horse flight behaviour between different zones and counts may result in poorer count accuracy and precision. The smaller population and range that horses now occupy provides DOC with an opportunity to make improvements in their population monitoring methods and adopt methods that were less feasible when the population was larger and more widely distributed.

We suggest that at least two different population monitoring techniques be employed that are independent and provide comparable size, growth and demographic data. If a method that uses aircraft is employed we recommend that the influence of the aircraft on horse behaviour be further investigated. If the current helicopter counting technique is retained then we recommend more detailed investigations of its accuracy and precision. However, the DOC helicopter counting technique is not used by feral horse population managers in other parts of the world; investigating its accuracy and precision is likely to be as costly and time-consuming as adopting alternative and better understood population sampling methods, but without the advantages of the alternative techniques. Aerial methods currently employed in North America could be evaluated for application in New Zealand. However, these methods may also give estimates that deviate dramatically from the true value and may variably under- and over-estimate population sizes (41% to 112% horse detection in different populations, Garrott *et al.* 1991a). Thus, the accuracy and precision of North American methods may also be poor.

Alternative methods of population size estimation include line or strip transects (Buckland *et al.* 1993), mark-resight or recapture (Pollock 1991), and dung density, deposition and decay (Barnes 1993) sampling methods. These methods are among the most rigorous of population size estimation methods available, our study has shown them to be feasible with the Kaimanawa population, and some of the remnant population is already marked (Cameron *et al.* 2001). These methods also have the advantage over helicopter count methods in that minor adjustments mean they may also provide demographic information (i.e. mark-recapture estimates of fecundity and survivorship for different age classes) and range use patterns (i.e. dung density measures). Monitoring range use, fecundity and survivorship, in addition to population size and change, may be particularly important if managers want to anticipate and control compensatory population growth after large population removals (evidenced by younger age at first breeding, higher foaling and survivorship) and immigration into adjacent regions cleared by muster. If the population is mustered every 2–3 years to remove individuals or administer contraceptives (see Cameron *et al.* 2001) then it would be possible to mark and release animals of known sex and age for mark-resight or recapture sampling. A record of marked animals re-sighted and re-mustered would provide the means to monitor annual recruitment, survivorship and population size and growth. This regime could be complemented with ground-based line transects every 2–3 years to measure horse density within their range. Line transects outside their known range could be used to monitor horse immigration and dispersal into protected habitat using measures of dung density, decay and deposition. This is one of many possible population monitoring regimes using better understood techniques that would provide better-quality information for the management of the Kaimanawa wild horse population and its impacts on vegetation in the long term.

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