Migration of feral pigs (*Sus scrofa*) in rainforests of north Queensland: fact or fiction?

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Abstract. The Wet Tropics bioregion of north Queensland has been identified as an area of global significance. The world-heritage-listed rainforests have been invaded by feral pigs (*Sus scrofa*) that are perceived to cause substantial environmental damage. A community perception exists of an annual altitudinal migration of the feral-pig population. The present study describes the movements of 29 feral pigs in relation to altitudinal migration (highland, transitional and lowland areas). Feral pigs were sedentary and stayed within their home range throughout a 4-year study period. No altitudinal migration was detected; pigs moved no more than a mean distance of 1.0 km from the centre of their calculated home ranges. There was no significant difference between the mean ($\pm 95\%$ confidence interval) aggregate home ranges for males ($8.7 \pm 4.3 \text{ km}^2$, $n = 15$) and females ($7.2 \pm 1.8 \text{ km}^2$, $n = 14$). No difference in home range was detected among the three altitudinal areas: $7.2 \pm 2.4 \text{ km}^2$ for highland, $6.2 \pm 3.9 \text{ km}^2$ for transitional and $9.9 \pm 5.3 \text{ km}^2$ for lowland areas. The aggregate mean home range for all pigs in the present study was $8.0 \pm 2.4 \text{ km}^2$. The study also assessed the influence seasons had on the home range of eight feral pigs on the rainforest boundary; home ranges did not significantly vary in size between the tropical wet and dry seasons, although the mean home range in the dry season ($7.7 \pm 6.9 \text{ km}^2$) was more than twice the home range in the wet season ($2.9 \pm 0.8 \text{ km}^2$). Heavier pigs tended to have larger home ranges. The results of the present study suggest that feral pigs are sedentary throughout the year so broad-scale control techniques need to be applied over sufficient areas to encompass individual home ranges. Control strategies need a coordinated approach if a long-term reduction in the pig population is to be achieved.

Introduction

An important requirement for effective feral pig (*Sus scrofa* Linnaeus, 1758) management is to obtain information on their temporal and spatial home ranges and locations and migration patterns (Giles 1980; Saunders and Kay 1991). The area over which control operations should be applied and the timing of control efforts to maximise effectiveness can be determined if home-range parameters and movement patterns are quantified (Caley 1997). Effective targeting of control efforts in locations where pigs are known to concentrate will reduce the costs and increase the effectiveness of control.

In Australia's Wet Tropics, rainforests have been identified as a refuge habitat of feral pigs (McIlroy 1993; Mitchell and Mayer 1997). There is also a perception among the rural community that pigs in the rainforest environment venture out to raid neighbouring agricultural crops and then return to the protection of the rainforest. Many landholders also hold the view that there are more pigs in the lowlands during the dry season than in the wet season (Mitchell and Mayer 1997). This has led to a perception of a seasonal migration of pigs from the highlands to the lowlands in the dry season and subsequent return migration from the lowlands to the highlands during the wet season. However, no studies have been undertaken to quantify the movements of pigs within the Wet Tropics region.

The following two aspects of movements of pigs were examined in the present study:

- potential migration of pigs between lowland and highland habitat areas in response to seasonal influences, and
- seasonal home-range patterns.

Materials and methods

Study site

The study site was situated near Cardwell, north Queensland ($18°16'S$, $146°2'E$). It was categorised into three broad macrohabitat types termed 'areas' (highland rainforests (above 800 m in elevation), the transitional ecotone between rainforest and the croplands on the lowlands, and the lowland coastal woodlands) (Fig. 1). A detailed description of the study site and areas are provided in Mitchell *et al.* (2007). The highland area was centred on a locality known as Society Flats ($18°12'30''S$, $145°45'30''E$). Two distinct locations were chosen to represent the transitional area, namely Kennedy Valley ($18°14'S$, $145°55'E$) and Upper Murray ($18°6'S$, $145°50'E$). The lowland area was situated in Edmund Kennedy National Park (EKNP) on the coastal lowlands ($18°14'S$, $146°E$).
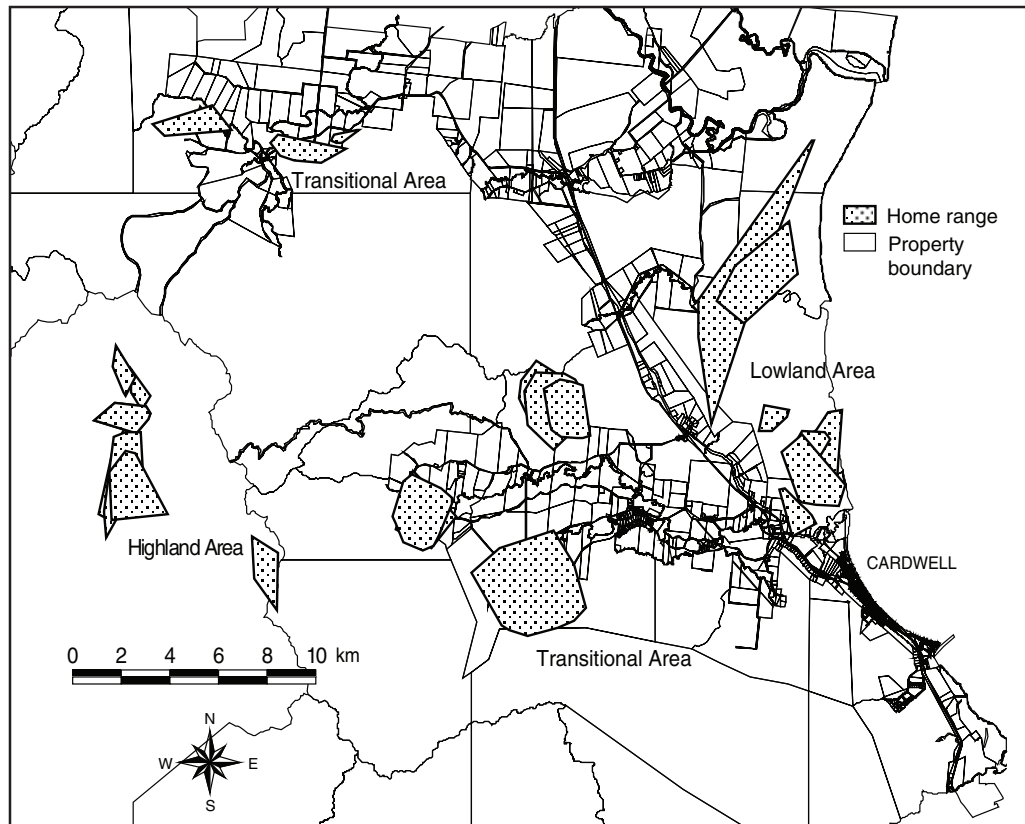
Fig. 1.   Map of the home-range boundaries of 29 radio-tracked feral pigs within the three areas of the study site.

Radio-tracking

Within the three study areas, adult pigs (>24 months of age) were trapped. Only adult pigs that had completed growth were collared to avoid strangulation, as there was limited opportunity to recatch and adjust collars. The captured pigs were sedated with Rompun (xylazine hydrochloride; Bayer Australia, Sydney) injected intramuscularly (2.5 mg kg^{-1} liveweight); dosage was calculated from visual weight estimation (Baber and Coblentz 1982). A second intermuscular injection of Ketamine 100 (ketamine hydrochloride; Mavlab, Brisbane) was applied at the rate of 3.0 mg kg^{-1} liveweight when the pig showed signs of lack of coordination. Each pig was weighed, aged by tooth-eruption patterns (Clarke *et al*. 1992) and photographed. Morphometric measurements were taken and a numbered plastic ear tag was attached to one ear for future identification purposes. A radio-tracking collar (Sirtrack Limited, Havelock North, New Zealand) was then secured firmly around the neck and the pig was released. Of the 41 pigs collared and released, 12 were subsequently deleted from the study; two pigs lost their collars, one died within 1 day of release, hunters caught seven and two moved into areas where their radio signals were masked by radio interference. The remaining 29 pigs (15 males and 14 females) were used for the analysis of altitudinal migration movement, and eight of these were also utilised in the seasonal home-range analysis on the rainforest boundary. Transmitter frequencies were in the 150–152-MHz range and battery life for each collar was ~18 months. Radio-tracking did not commence

until 1 month after collaring, to allow the animals to resume normal behaviour.

Location fixes were obtained by taking bearings from 78 fixed stations of known coordinates that were scattered throughout the study site. Bearings from three to five stations were obtained for each fix for each pig where possible, to enable triangulation of the pig's location, and to establish the area of the bearing error ellipse polygon with the software program Locate II (Nams 2000). When pigs were very close (within 500 m) to stations, only two bearings were required because the location error would be very small (White and Garrott 1990). Bearings were obtained with a portable scanning receiver and standard three- or four-element 'Yagi' aerials, either mounted on a tower in the back of a vehicle or held in the hand. Bearings were obtained with the system of Saunders and Kay (1991) by determining the direction at which the strongest signal (peak) was obtained and then determining the direction at which the signal was inaudible (null) to the left and right of the peak signal. The magnetic bearing of the transmitter was then the line bisecting the angle between the two null bearings.

As only one observer was available at each bearing fix, simultaneous bearings could not be obtained. The observer drove to different stations until a signal and bearing fix was obtained, and then rapidly drove to other nearby stations to obtain cross bearings. The time taken to obtain the location fixes was minimised as much as possible, varying from 1 min to a maximum of 10 min. Stations were selected that were as close to an animal's

estimated position as possible and at obtuse angles to the original bearing, to reduce location error (White and Garrott 1990).

The position of each pig was estimated with the program 'Locate II' after each bearing was corrected for magnetic deviation (8°). Location fixes were the centre point of a 95% error ellipse estimated with the Lenth maximum likelihood estimator available in LOCATE II, as described in White and Garrott (1990). Location fixes were scrutinised for outliers on the basis of field notes on signal strengths and an animal's estimated distances from the stations. Observers were trained before recording data by locating collars attached to wooden pegs in different locations that were unknown to the observers.

Migration movements and overall home ranges

Migration patterns were determined by obtaining periodic fixes of the location of collared pigs during the battery life of the collar. Of the 29 pigs radio-tracked, seven (3 males, 4 females) were initially captured in the highland area, 10 (5 males, 5 females) in the transitional area and 12 (7 males, 5 females) in the lowland area. The length of tracking time for each pig varied (6–33 months), with a mean tracking period of 13.1 months (2.5 location fixes per pig per month). Location fixes were obtained in both the wet and dry seasons. In total, 940 location fixes were obtained from all pigs, with a mean of 34 location fixes (range 7–137). A location fix for each pig was attempted two or three times per month, or whenever the observers were within the areas. Cyclones, restricted access because of weather conditions and landslides, and thick vegetation restricting signal strength combined to make accurate periodic positional fixes on pigs in remote mountain locations in the highlands difficult to obtain.

When pigs with known active collars could not be located, an aerial search was initiated. Aerials were attached to the wings of a Cessna 207 fixed-wing light aircraft, which then flew over the last known location of the missing pigs. The pig location was estimated by the method of White and Garrott (1990). No location error could be calculated by this method.

Location data were analysed with the Ranges V program (Institute of Terrestrial Ecology, Wareham, UK). Home-range estimates were derived from the 'minimum convex polygon' (MCP) analysis. This method is strongly influenced by peripheral fixes, so a peeled polygon analysis based on 95% of range fixes was used to eliminate the outermost 5% of fixes (White and Garrott 1990). The harmonic mean fix estimate for each pig was calculated to estimate the harmonic centre (Hc) of range activity, the maximum range span distance and the mean distances of fixes from the calculated Hc (Dixon and Chapman 1980). This method calculated the mean distances that pigs moved from their home-range centres.

A home range was calculated for each of the 29 radio-collared pigs by using the combined location fixes obtained for each pig during the battery life of its collar, to test the hypothesis that individual pigs migrate between the lowland and highland habitats. Movement distances from home-range centres that were greater then twice the mean diameter of the calculated home range would be defined as a migration movement between the highland and lowland areas. The relationship

between the number of fixes and the derived home-range area was examined by regression analysis.

A two-way ANOVA of home ranges was used to test for differences among the three areas, the genders and a gender by area interaction. Another hypothesis tested was that there was gender difference in variation in home range within areas. Since numbers were too small to estimate variances separately for each area, a pooled estimate of variance was estimated across the three areas for each gender (with a one-way ANOVA).

Also because the male pigs in the study were generally larger than the female pigs, a regression analysis of data from each gender was done separately to test whether pig size influenced home range.

Seasonal home ranges

Seasonal home-range calculations in the highlands rainforests were not practical as sufficient location fixes to derive a seasonal home range could not be obtained. Transmitter signals were limited by the thick vegetation, and limited access often prevented the observers from approaching close enough to the collared pigs to receive accurate signals. Only two pigs (one male and one female) in the lowland area and six pigs (three males and three females) in the transitional area had more than 30 location fixes within a defined season, as required for calculation of seasonal home ranges. MCP analysis is typically stable after this number (White and Garrott 1990).

Location fixes for each season were obtained during continuous 72-h tracking sessions that were repeated three times during three continuous weeks in the dry season (November), and the procedure was repeated in the wet season (February). Fixes were obtained at 3-hourly intervals (storm activity and flooding prevented some location fixes from being obtained), commencing at 0900 hours for the first 24 h, 1000 hours for the next 24 h and 1100 hours for the last 24-h tracking period. Thus, during the 72-h sessions, 24 location fixes for each pig were attempted, corresponding to a fix location for each hour of the day. Because of the time difference between obtaining bearings (minimum of 1 to a maximum of 10 min), bearings for each pig were obtained in the same order for each tracking session to keep time differences between fixes for each individual pig constant. Aggregate and seasonal home-range estimations were calculated as above by the 95% MCP method (White and Garrott 1990).

Increment area plots were examined to see whether the home range was influenced as successive location fixes were added. This was used to test the relationship of home range (% of range area) with the cumulative numbers of fixes. A sufficient number of fixes to accurately estimate a home range occurred when this relationship plot approached an asymptote. Only data that approached an asymptote were used in home-range estimations. The harmonic mean fix for each home range within each season was calculated to examine whether a shift in home-range centres occurred in response to changing seasons.

Since the eight pigs were measured during consecutive seasons, their home ranges were analysed as a gender × season factorial (ignoring differences between lowland and transitional areas) with a repeated-measures ANOVA. Because of the small

size of the dataset, the statistical power of this analysis was quite low.

Results

Location error

Error estimations for individual location fixes for the migration study were unable to be calculated. Estimations of location fixes from the air, with only signal strength as the indicator, and the difficulty of obtaining multiple bearings from pigs in remote areas precluded location-error estimations to be obtained. For the seasonal movement study, the overall mean bearing-error angle for 238 location fixes obtained from seven pigs was 3.08° (95% C.I. = 6.16°) and the mean area of the 95% error ellipse around 229 location fixes was 10.17 ha. The mean location error was 68 m (maximum 136 m) at 1 km from the antenna. As most fixes were estimated to be less then 1 km from the location stations, this level of precision was considered sufficient for the aims of the present study.

Migration movements

An individual pig's home range and the mean distance it moved from its calculated home-range Hc during the total time each pig was followed are presented in Table 1. No pigs were located

Table 1.   The home ranges for 29 feral pigs that were radio-tracked within three altitudinal areas of the Wet Tropics rainforests

The bodyweight and the mean distance individual pigs moved from the harmonic centre (Hc) of their home range are also given

Area	Sex	Weight (kg)	Home range (km^2)	Mean distance from Hc
Highland	M	92	4.6	0.73
	M	96	3.8	0.63
	M	105	6.0	0.72
	F	85	10.1	1.8
	F	91	9.7	1.09
	F	85	9.5	1.72
	F	70	6.6	1.07
Transitional	M	58	6.8	0.88
	M	78	2.8	0.36
	M	83	21.2	1.1
	M	75	4.9	0.75
	M	65	4.7	0.8
	F	53	3.2	0.34
	F	46	7.2	0.92
	F	65	3.1	0.6
	F	72	3.7	0.88
	F	46	4.5	0.97
Lowland	M	83	15.4	1.6
	M	65	4.0	0.5
	M	65	4.1	0.67
	M	98	10.0	0.74
	M	42	4.5	0.57
	M	80	4.9	1.2
	M	100	33.1	5.8
	F	55	10.1	1.29
	F	66	5.9	0.77
	F	25	4.2	0.98
	F	64	13.1	1.0
	F	50	9.3	0.89

outside of their initial area of capture at any time during the study. No movements in relation to the altitudinal gradient between the lowland area and highland area were observed for any of the collared pigs. The home ranges (calculated during the whole period of the study) for all pigs are presented in Fig. 1. Eight home-range estimations were based on fewer than 10 location fixes. However, as there was no significant ($P = 0.15$) linear regression between the number of location fixes and the home-range size for all studied animals, they were included in home-range estimations.

The two-way ANOVA of individual home ranges showed no significant area × gender interaction ($F_{2,23} = 0.81$, $P = 0.46$), no significant difference between areas ($F_{2,23} = 0.92$, $P = 0.41$) and no significant differences between genders ($F_{1,23} = 0.27$, $P = 0.61$). Means (and 95% confidence intervals) for the areas were highland 7.2 ± 2.4 km^2, transitional 6.2 ± 3.9 km^2 and lowland 9.9 ± 5.3 km^2, and for genders 8.7 ± 4.3 km^2 for males and 7.2 ± 1.8 km^2 for females. The overall mean home range for all pigs in all areas was 8.0 ± 2.4 km^2.

The pooled variance estimate for home range (across the three areas) for male pigs was 75.0 (12 d.f.) and for female pigs just 6.2 (11 d.f.). These variances were significantly ($F_{12,11} = 12.1$, $P < 0.01$) different. The increased precision in the female data in the one-way ANOVA resulted in the mean home range in the transitional area of 4.3 being significantly lower than those in the highland and lowland areas (9.0 and 8.5 respectively).

The average weight for males was 79 kg and for females, 62.4 kg (Table 1). For male pigs, the heavier animals tended to have larger home ranges. The linear regression coefficient was 0.18 and significant at $P = 0.15$. For female pigs this trend was much less pronounced (coefficient 0.07, $P = 0.17$).

The average and maximum distances that pigs moved from their centre of activity (harmonic mean fix of the home range) are presented in Table 2. The mean distance any pig in any area moved from their harmonic mean fix was 1.03 km; the mean maximum distance any pig moved from the Hc was 2.64 km.

Seasonal home range study

The number of location fixes obtained for eight pigs in total was sufficient for the home ranges of only seven pigs (4 males and 3 females) to be calculated in the dry season and for six pigs (3 males and 3 females) in the wet season. A repeated-measures analysis of home ranges, with season as the repeated measure, showed no significant main effects of gender ($F_{1,6} = 0.16$, $P = 0.70$) or season ($F_{1,3} = 2.34$, $P = 0.22$), nor a significant interaction between gender and season ($F_{1,3} = 1.45$, $P = 0.31$). However, the statistical power of the analysis was low, because of

Table 2.   The mean and maximum distance (km) male and female feral pigs moved from the harmonic mean centre (Hc) of their home range within each of the three study areas

Area	Distance from Hc			
	Male		Female	
	Mean	Max	Mean	Max
Highland	0.69	1.78	1.42	3.13
Transitional	0.78	2.64	0.74	2.05
Lowland	1.58	3.86	0.99	2.38

the small dataset. Mean home ranges were $7.7 \pm 6.9\,\mathrm{km}^2$ in the dry season and $2.9 \pm 0.8\,\mathrm{km}^2$ in the wet season.

The harmonic mean fix for each home range within each season was plotted to examine whether home-range centres moved between the seasons. As the mean distance between the Hc seasonal home ranges were 651 m (range 539–806 m) for males and 250 m (range 141–360 m) for females, no large-scale relocation of home-range centres between the seasons was observed.

Discussion

Two aspects of feral-pig movement patterns within the World Heritage Area were investigated in the present study. The first was large-scale migration-type movement patterns, of which no evidence was found. No movements between the altitudinal gradients (highlands to lowlands) were observed, as no collared pig was observed to move away from its initial capture site. All movements from individual home-range centres averaged slightly more than 1 km, a distance well within normal home-range boundaries. The second was migration in response to seasonal conditions, which was not observed among six pigs that had fix locations in both the wet and dry seasons.

The absence of large-scale migration movements by feral pigs has been found in studies in other environments. Caley (1997) established that pigs are relatively sedentary in the Northern Territory, with a mean recapture distance of 3.2 km for males and 1.8 km for females; normal movements with their home ranges. Similarly, Giffin (1978) found small recapture distance (1.1 km for males and 1.4 for females) in Hawaiian rainforests. Hone (1988) found significant seasonal altitudinal movement in his study in Canberra which may be due to very cold temperatures (including snow) in winter forcing pigs to migrate to warmer lower altitudes. The absence of marked changes in factors such as temperature between different altitudes or seasons in this rainforest environment may explain why altitudinal shifts were not observed in the present study.

All home ranges found in both aspects of the present study were within the limits of those in the past Australian studies, in a variety of habitats, which vary from 1.4 to 43 km^2. The home ranges in the present study were similar to those of other studies in habitats where water, cover and food resources were not limiting (McIlroy and Saillard 1989; Dexter 1998). For studies in habitats that lacked water, cover or food resources, the home ranges were generally larger than those found in the present study (Giles 1980; Caley 1993). Home ranges in the present study were generally larger in area than those in overseas studies (Diong 1982; Singer *et al.* 1981; Baber and Coblentz 1986).

The mean home-range estimation for all areas and both genders combined was 8.0 km^2. Dexter (1999) had similar home-range sizes in his study in the semi-arid areas, although he found a significant gender difference (males 7.9–11.6 km^2 and females 4.2–8.0 km^2). Saunders and Kay (1991) also found that male home ranges were significantly larger than those for females. The only significant differences in home ranges in the migration study were that males exhibited more animal to animal variation within areas than did females (pooled variances of 75.0 and 6.2 respectively), and females in the transitional areas had a

significantly ($P = 0.03$) smaller mean home range (4.3) than did those in highland and lowland areas (9.0 and 8.5 respectively). Because of the greater variation in male home ranges, no significant pattern could be detected. The incorporation of a crop food resource within the transitional area home range may explain the female difference as home range is dictated by resource availability. Dexter (1999) found females varied their home ranges in response to varying food abundance as a home range contains a finite potential energy resource that is proportional to its area (Harestad and Bunnell 1979). Mammals adapt to this variation in food availability by maintaining a home range with sufficient resources when food is limiting. The associated seasonal home-range study discussed below also found no significant gender differences, although the home-range size difference was more pronounced than in the migration study. The lack of gender differences in this unique rainforest environment is difficult to explain without a more detailed study. A general over-abundance of resources in the rainforests may mean that males do not require a larger area to satisfy their energy requirements than do females; however, this was not tested in the present study.

Male home ranges varied greatly (from 2.9 km^2 minimum to 33.1 km^2 maximum). Two of the larger males (83 kg and 100 kg) had the largest ranges of 21.2 km^2 and 33.1 km^2 respectively. Large boars have been found to be more likely to disperse across distance (>30 km) in search of breeding opportunities (Saunders and Kay 1991; Hampton *et al.* 2004; Spencer *et al.* 2005). Dexter (1999) found males maintained a large, unvarying home range to maximise access to females. The movements of these solitary boars may have implications for management plans. Trapping systems, for example, will have to take into account the large distances mature boars may move between refuge areas and the crops they are damaging. The larger than normal movements of these solitary boars may also have implications in containment of exotic disease outbreaks through enhancing the transmission coefficient of disease through a population (Dexter 2003).

Home range has also been directly associated with animal body mass; larger animals tend to have higher resource requirements and thus need to forage across larger areas (Lindstedt *et al.* 1986; Saunders and McLeod 1999). The larger males in the migration study tended to have increased home range ($P = 0.15$). The mean body mass was 79.0 kg for males and 62.4 kg for females; however, no significant differences in the home ranges between the sexes were found. Other studies have also found that males tend to have larger aggregate home ranges than do females (Barrett 1978; Giles 1980; Baber and Coblentz 1986; Caley 1997; Dexter 1999).

The second aspect of the present study was to assess the seasonal influence on home range. This analysis was possible only on the rainforest boundary because of access and adverse topography restrictions. No statistically significant seasonal effects were found, although the combined gender mean home range in the dry season (7.7 km^2) was more than twice that in the wet season (2.9 km^2). Home ranges for males (2.8 km^2) and females (3.0 km^2) were similar in size in the wet season, whereas in the dry season the home ranges for males (9.8 km^2) were generally larger than those for females (4.9 km^2). The large variations in the male home ranges may have obscured any differences that may have existed between the seasons in the

present study. Saunders and Kay (1991) found a seasonal difference in their study, with the home range being greatest in winter and smallest in autumn. They attributed this difference to variations in food availability. Other studies (Lindstedt _et al._ 1986; Massei _et al._ 1997; Dexter 1999; Lemel _et al._ 2003) have suggested that the size of home range may be influenced by other factors such as age, sex, physiological status, energy requirements, ambient temperature, population density and hunting pressure.

The overall mean aggregate home ranges of males ($6.8\,km^2$) and females ($4.0\,km^2$) obtained in the seasonal-movement study in the transitional area are comparable to home ranges obtained in the transitional area from the migration study ($6.2\,km^2$). The individual home-range centres did not shift between the wet and dry seasons, rather the home ranges expanded in size during the dry season, especially for males. The shift in the geographical centres of home range between the seasons averaged 651 m for males and 250 m for females in the present study, well within normal home ranges. This supported the findings of the migration study where movement distance between the centres of home-range activity was not significant. All home ranges were irregular in their configuration and overlapped each other in both seasons. Saunders and Kay (1991) also found that aggregate home-range boundaries extensively overlapped for both males and females in their study.

The absence of large-scale movements that could be termed migration is contrary to the general community perception that feral pigs inhabit the highlands during the wet season and migrate to the coastal lowlands during the dry season to forage on the ripening sugarcane and banana crops. These pigs then return to the highlands in the wet season when the sugarcane is harvested (McIlroy 1993; Mitchell and Mayer 1997). The results of the present study do not support this seasonal migration perception. Feral pigs inhabiting the rainforest–crop boundary are most likely the cause of this migration perception. The seasonal home-range study found that feral pigs (especially the males) move across larger areas in the dry season, possibly because of decreased food and water availability. Larger foraging areas in the dry season may increase the probability of contact with people, especially during the sugarcane harvest period. The community perception is that pig populations within crops had increased and that the pigs had to come from somewhere, namely the highland rainforests. During the wet season, home ranges tend to be smaller and human activity within crops is reduced, so the probability of contact with people is less. The community perception is that the pig population within the crops has decreased and hence the pigs must have moved back to the highland rainforests.

The results of the present study suggest that the community perception of a seasonal migration pattern occurring from the highland to the lowlands is unfounded in the study area. The seasonal changes in movement patterns of pigs within their normal home range on the crop and rainforest boundary are the cause of this community perception. The home range and movement data suggest that control strategies need a coordinated approach if a long-term reduction in the pig population is to be achieved. Pigs are sedentary throughout the year so broad-scale control techniques need to be applied over sufficient areas to encompass individual home ranges.

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