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Population demography of Australian feral bees (*Apis mellifera*)

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Abstract Honey-bees are widespread as feral animals in Australia. Their impact on Australian ecosystems is difficult to assess, but may include competition with native fauna for floral resources or nesting sites, or inadequate or inappropriate pollination of native flora. In this 3-year study we examined the demography of the feral bee population in the riparian woodland of Wyperfeld National Park in north-west Victoria. The population is very large but varied considerably in size (50–150 colonies/km^2) during the study period (1992–1995). The expected colony lifespan for an established colony is 6.6 years, that for a founder colony (new swarm), 2.7 years. The population is expected to be stable if each colony produces 0.75 swarms per year, which is less than the number predicted on the basis of other studies (2–3 swarms/colony per year). Therefore, the population has considerable capacity for increase. Most colony deaths occurred in the summer, possibly due to high temperatures and lack of water. Colonies showed considerable spatial aggregation, agreeing with earlier findings. When all colonies were eradicated from two 5-ha sites, the average rate of re-occupation was 15 colonies/km^2 per year. Ten swarms of commercial origin were released and were found to have similar survival rates to founder colonies. However, the feral population is self-sustaining, and does not require immigration from the domestic population.

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Introduction

The European honey-bee, *Apis mellifera*, was introduced to Australia in 1822 (Hopkins 1886) and has become widely distributed as a feral animal. Feral honey-bee colonies can reach extremely high densities in some Australian environments. For example, Oldroyd et al. (1994) estimated that there were 77.1 colonies/km^2 in the riparian woodland of Wyperfeld National Park in north-west Victoria. Although densities of this magnitude are unlikely to be common, there is potential for adverse interactions between feral bees and native flora and fauna at any density because of overlap in resource use (Pyke 1990; Aizen and Feinsinger 1994; Oldroyd et al. 1994). Key areas of concern have been reviewed by Pyke (1990), Paton (1993, 1996) and Sugden et al. (1996) and are outlined below.

First, feral honey-bees may reduce the population of native pollinators and nectar and pollen feeders through competition for nectar and pollen (Sugden et al. 1996). Honey-bees are efficient foragers, and reduce standing crops of nectar (Paton 1989, 1993) and pollen (Vaughton 1996). Studies have shown that competition and resource partitioning can occur among bee species for floral resources (Schaffer et al. 1979, 1983; Roubik and Buchmann 1984; Roubik et al. 1986; Oldroyd et al. 1992). Reduction in standing crops of nectar may also adversely affect bird pollinators (Paton 1993). However, a demonstration of potential competition for floral resources does not necessarily result in a reduction in reproductive success of native pollinators, or a long-term decline in their numbers. For example, long-term studies of native bee abundance in central America after the arrival of Africanized bees did not reveal any decline in their numbers (Roubik 1983, 1988; Roubik et al. 1986). Donovan (1980) suggested that prolonged contact with European bees has had little effect on the native bees of New Zealand (although it is difficult to see how such impacts can be assessed after 140 years of interaction). Further, experimental additions of honey-bees to sites in southern New South Wales (Sugden and Pyke 1991) and south-west Victoria, Australia (M.P. Schwarz et al. cited in Sugden et al. 1996) did not reduce the reproductive success of native bees; indeed, reproductive success of native species was slightly increased, possibly due to reduced predator pressure on native species (M.P. Schwarz personal communication).

Second, honey-bees may compete for nest sites with native fauna (Oldroyd et al. 1994). Although the number of tree hollows available as nest sites for bees and native fauna is large in many Australian habitats (Saunders et al. 1982; Oldroyd et al. 1994), there is potential for competition for this resource (Coelho and Sullivan 1994; Oldroyd et al. 1994; Lawler et al. 1995). Oldroyd et al. (1994) found that 50% of the hollows selected by honey-bees were also suitable for regent parrots (*Polytelis anthopeplus*), a threatened species. Coelho and Sullivan (1994) found that 30% of nest boxes placed for native wildlife in Illinois were occupied by honey-bee swarms in one season.

Third, as plants and their pollinators often coevolve, an exotic species may reduce the efficiency of pollination in some instances, and reduce the reproductive success of plants. For example, *Grevillea* spp. are adapted for bird pollination and may not be adequately pollinated by honey bees (Taylor and Whelan 1988; Vaughton 1996), although pollination may not be a limiting factor in seed set. Paton (1993) demonstrated that honey-bee foragers are less efficient pollinators of *Correa* and *Callistemon* than native birds.

The extent to which feral honey-bees adversely affect Australian biota remains unclear and is the subject of continuing research (Sugden et al. 1996). However, it is almost certain that while the effects of feral bees may not be as significant as has sometimes been feared (Pyke 1990), they are likely to be non-zero. Therefore, mitigation of feral honey-bee populations in preserved ecosystems would seem a desirable objective.

Here we report on the population dynamics of a population of feral honey-bees in Wyperfeld National Park (35°35′40" S, 141°55′05" E) in north-west Victoria, Australia. Our objectives were to determine (1) the size of the population, (2) whether it would be feasible to control the population, (3) whether the existing population is self-sustaining or whether it requires supplementation via swarms which escape from commercial colonies, (4) how quickly depopulated areas are re-colonised, (5) whether commercial swarms can survive in this area, and (6) whether the finding of Oldroyd et al. (1995) that *Apis mellifera* colonies show an aggregated spatial distribution is repeatable over time.

Materials and methods

Study site

We surveyed the feral honey-bees in Wyperfeld National Park. The arboreal vegetation is primarily mallee or banksia heathland, not exceeding 10 m (Garnett 1965) and mostly of insufficient mass to accommodate a beehive. However, in many years the mallees (*Eucalyptus dumosa*, *E. gracilis*, *E. incrassata* and *E. oleosa*) and the banksia (*Banksia ornata*) provide continuous and abundant nectar and pollen forage for honey bees (Goodman 1973).

In the southern section of the park, Outlet Creek connects a series of shallow lake beds (see Fig. 1 in Oldroyd et al. 1994, 1995). It drains the Wimmera River system but rarely flows, the last time being 1975 (Anon 1991). Narrow bands of red gum (*E. camaldulensis*) and black box (*E. largiflorens*) are present along the creek and associated lakes. Mature red gum and black box trees are very large and develop cavities suitable for nesting by honey-bees and native fauna. A few other tree species (*Callitris* spp., *E. leucoxylon*) in the park occasionally also have suitable cavities.

Bee-keeping was practised in the park from approximately 1930–1970, after which the number of sites available to bee-keepers was steadily reduced. No bee-keeping has been permitted except on the periphery of the park since 1980. The population of feral bees in the narrow band of riparian vegetation that borders Outlet Creek was estimated to contain 77.1 colonies/km^2 (Oldroyd et al. 1994), and these colonies tend to have a clumped distribution (Oldroyd et al. 1995).

Survey method

Seven study sites 100 m × 500 m were established along Outlet Creek (see Oldroyd et al. 1994, 1995). A plot was established at each study site, located away from public view. Each plot encompassed the red gum/black box woodland. Plots were each divided into five 10,000-m^2 sectors within which each tree greater that 1 m in circumference at breast height was tagged with a numbered aluminium tag (Permotags, Hortico, Laverton, Australia). Preliminary surveys revealed no hollows in trees less than 1 m circumference. The plots contained 283.3 ± 28.3 (SE) trees (Oldroyd et al. 1994).

Plots were initially surveyed in March and April 1993 (Oldroyd et al. 1994). Pairs of observers walked around each tree and counted the number of bee colonies from four compass points. Maps were prepared of the location of each colony within the plots, and trees and hollows occupied by bees were identified with conspicuous paper tape. Additional bee colonies were located outside the plots by fortuitous discovery and direction from park rangers.

In September 1994 and 1995, before swarming began, all colonies (including those found outside the plots) were resurveyed to determine which had died during the winter. All trees within the plots were resurveyed in November or December (after swarming) to ascertain the location of new swarms. All colonies were surveyed in March 1994 and April 1995 to determine which colonies had died during the summer.

Observations were only made when temperatures exceeded 16°C and when known colonies were observed to be foraging freely. Colonies were assumed to be alive if they fulfilled any of the following criteria: (1) they defended the nest entrance when disturbed; (2) a pollen forager was seen, and (3) regular, purposeful flight movements were seen. Colonies were assumed to be dead if: (1) observers were not attacked after repeatedly striking the nest entrance or blowing in it; (2) flight was erratic with bees circling around the hollow entrance, suggesting water foragers (many hollows in *E. camaldulensis* contain pockets of water which are used by bees; Oldroyd et al. 1994), and (3) flight was erratic around the entrance, no pollen foragers were seen after constant observation, or fighting was seen, indicating that a recently deceased nest was being robbed out. Whenever there was some doubt about the status of a colony, we went to considerable lengths to determine the state of the nest. This usually involved beating the nest entrance, or where this was not possible, protracted (5–10 min) observation of the nest entrance through binoculars.

Experimental manipulations

To determine if bees of commercial origin can survive at Wyperfeld, sites 1 and 4 were randomly selected for a release experiment. We released ten swarms of bees of commercial origin (probably *A. mellifera ligustica*) on 2 November 1993, late in the natural swarming period. Approximately 2 kg of bees was placed together with their accompanying queen (temporarily constrained in a mailing cage; Laidlaw and Eckert 1962) in tree cavities which were judged by us to be suitable for beehives, and similar to typical cavities utilised by bees in Wyperfeld (Oldroyd et al. 1994). A description of the cavities selected is given in Table 1.

To determine how quickly an area cleared of bee colonies would be recolonised, sites 2 and 6 were randomly selected for bee eradication. Colonies were killed by fumigation with phosphine gas generated from aluminium phosphide tablets on 27 August 1993. All new colonies found at these sites during subsequent surveys were also killed.

Statistical analysis of survival

Survivorship of colonies was compared across seasons by analysis of 2 (season) × 2 (outcome; alive or dead) contingency tables using Fisher's exact test. The survivorship of established and founder colonies was also compared in the same way.

Table 1 Characteristics of cavities selected for release of swarms

Site	*Eucalyptus* tree species	Aspect of opening	Dimensions of opening (cm)	Estimated volume (l)	Height (m)
1	*E. camaldulensis*	South	12 × 15	20	6.5
	E. largiflorens	South	10 × 10	100+	3.5
	E. largiflorens	South	16 × 20	300–400	2.5
	E. camaldulensis	North-east	12 × 26	100	4
	E. camaldulensis	South	9 × 15	40	6
4	*E. camaldulensis*	North-east	15 × 15	30+	14
	E. camaldulensis	North	25 × 25	32	21
	E. largiflorens	South-west	15 × 15	1,000	9
	E. camaldulensis	South	12 × 16	100	18
	E. largiflorens	East	10 × 16	20	15

Results

Distribution and density of colonies

The estimated density of colonies varied greatly over time from an estimated peak of 148 colonies/km^2 in September 1994 to a low of 40 colonies at the end of the study (Fig. 1). The estimate for April 1993 may be low because some established colonies may not have been found in the initial surveys.

The location of each colony in sites 1, 3, 4, 5 and 7 in the November/December survey period of each year was determined and is symbolically represented in Fig. 2. Sites 2 and 6 are excluded because colonies were killed by us at those sites, and colonies experimentally added by us at sites 1 and 4 are also excluded (the location of the nests at sites 2 and 6 are given in Oldroyd et al. 1995).

If a group of organisms is randomly distributed in the environment, the pattern of occurrence is expected to be Poisson distributed, with variance in numbers of or-

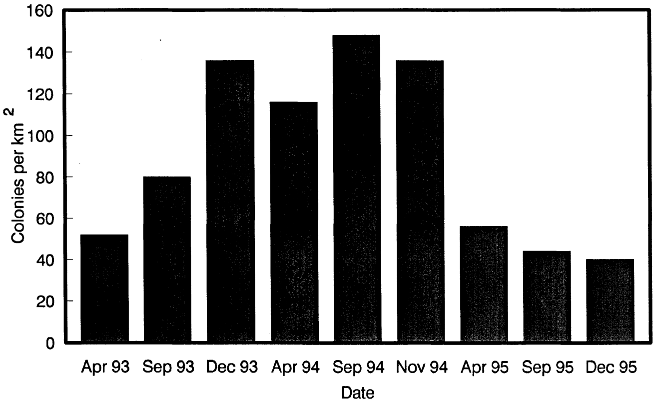
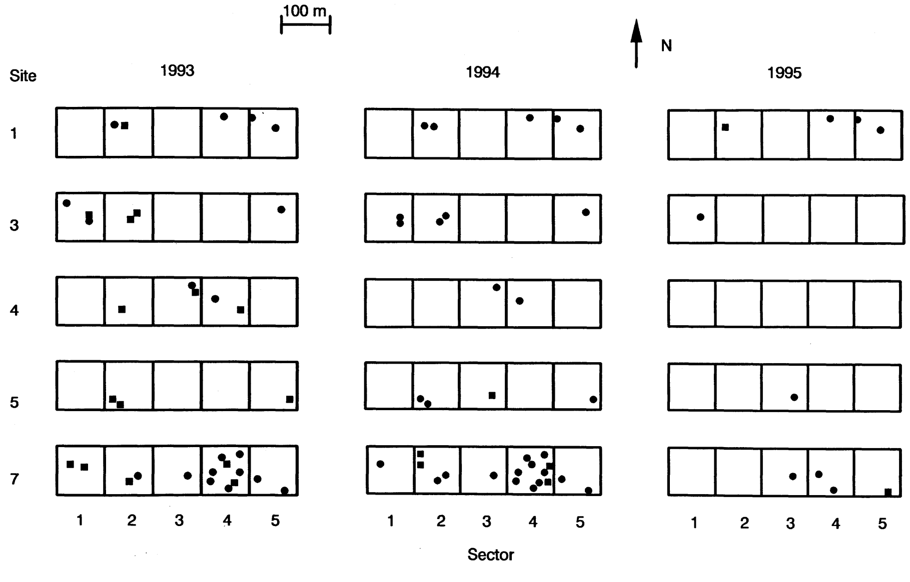


Fig. 1 Estimated density of feral honey-bee colonies in Wyperfeld National Park per square kilometre for 1993–1995

Fig. 2 Spatial distribution of colonies at the early summer surveys (*circles* established colonies, *squares* founder colonies)



ganisms per sampling unit expected to be approximately equal to the mean number of organisms per sampling unit. Alternatively, if the pattern of occurrence is clumped, then it is expected to follow the negative binomial distribution, with the variance in the number of organisms per sampling unit larger than the mean (Zar 1974; Ludwig and Reynolds 1988). The number of sampling units (sectors in Fig. 2) is insufficient to allow us to test the goodness of fit of our data to these distributions as a statistical test of the hypothesis that the colonies were aggregated. For a small number of sampling units, a statistical test of aggregation is the significance of the deviation of the index of dispersion (ID) from unity. ID has the value $\frac{s^2}{\bar{x}}$, where s^2 and $\bar{x}$ are the variance and mean of the number of organisms per sampling unit. According to Ludwig and Reynolds (1988), ID is distributed as χ^2, and a test statistic is:

$$\chi^2 = \mathrm{ID}(N-1)$$

where N is the number of sampling units and the degrees of freedom are $N-1$ (Ludwig and Reynolds 1988). Aggregation is dependent on scale, so we made two calculations of ID for each survey, one based on sectors and one based on sites as the sampling unit. By this test, colonies were highly aggregated in 1993 and 1994, whether sectors or sites were used as the sampling unit (note these are not independent analyses). In 1995, there were too few colonies to make a reliable estimate of ID (Table 2).

Colony survivorship

Following Seeley (1978), two categories of colonies were defined. Established colonies were categorised as those that had survived a winter, whereas new swarms were categorised as colonies that had not overwintered. Some ambiguity exists in this classification for colonies found before December 1993. First, all of the colonies found in the preliminary surveys of April and June 1993 were classified as established, when, doubtlessly, some were swarms from spring 1992. Second, some of the 8 new colonies found in September 1993 were very likely not overwintered colonies, but very early swarms. These 8 colonies were thoroughly examined for signs of long-term occupation (e.g. propolis or signs of wear or travel staining around the entrance hole, where comb was visible or could be retrieved with bent wire, the presence of old combs). Five of these were classified as established nests, while 3 were classified as new swarms. We believe our classifications are correct, although some doubt must remain. Subsequently, all new colonies were classified as new swarms. The frequency and thoroughness of surveys (and our increasing skill levels) means that it is extremely unlikely that established colonies within the plots were unknown to us after December 1993.

Another possible source of ambiguity is undetected reoccupation (Seeley 1978). We detected at least five reoccupations during this study, so some colonies we classified as established may have been new swarms which took up residence in a previously used cavity.

Established colonies survived significantly better than founder colonies in the summer of 1993, but at all other times the survivorship of founder and established nests was similar (Table 3). Survivorship was strongly influenced by year. The summer of 1994 claimed 40% of established colonies and 25% of (fewer) founder colonies, whereas all established colonies survived the summer and winter of 1993. This may have been due to poor rainfall and high summer temperatures in 1994. Average rainfall at the campground near the centre of the study

Table 2 Tests of aggregation of honey-bee colonies in Wyperfeld National Park

Date of survey	Number of colonies	Sampling unit based on sectors ($df = 24$)			Sampling unit based on sites ($df = 5$)		
		ID	χ^2	P	ID	χ^2	P
Dec 1993	34	2.07	49.82	0.001	3.26	13.26	0.023
Nov 1994	34	3.12	74.82	< 0.001	5.98	23.94	< 0.001
Dec 1993	10	1.04	25.00	0.41	1.40	7.00	0.22

Table 3 Summer and winter survivorship of feral colonies in Wyperfeld National Park. *Established colonies* are those which have survived at least one winter. *Founder colonies* are those resulting from the swarms of the specified season. *Alive* indicates those colonies that entered the specified period that survived to the end of that period. *Dead* identifies those colonies that entered the specified period that did not survive to the end of that period. *Survival* is the proportion of colonies that entered the period that survived to the end of that period. *P* represents the probability that founder and established colonies had the same survivorship (Fisher's exact tests from two-way contingency tables). Most colonies in the winter 1993 group were first observed in April 1993. This group includes both founder and established colonies because their status was unknown at the beginning of the study. See text. Data for summer 1995 are incomplete because the study terminated before its end

Season	*Established colonies*			*Founder colonies*			P
	Alive	Dead	Survival	Alive	Dead	Survival	
Winter Jul–Sep 1993	35	0	1.0	–	–	–	–
Summer Sep 1993–Apr 1994	35	2	0.94	14	10	0.58	0.002
Winter Apr–Sep 1994	33	0	1.0	14	0	1.0	1.0
Summer Sep 1994–Apr 1995	18	29	0.38	3	9	0.25	0.51
Winter Apr–Sep 1995	12	6	0.67	1	2	0.33	0.53
Summer Sep–Dec 1995	9	4	0.69	–	–	–	–

area for the years 1977–1994 was 330 mm (range 91.5–479.4 mm; park records provided by D. Martin). In the drought of 1994, 139 mm was recorded, one of the lowest rainfalls since records had been kept. Rainfall in 1993 was normal at 383 mm.

Established and founder colonies were more likely to die in summer than in winter in all years ($P = 0.0001$, 0.003 and 0.001 for the 1992/1993, 1993/1994 and 1994/1995 seasons, respectively). However, when founder colonies are excluded from the analysis, this difference only held for the winter of 1993 compared to the summer of 1993/1994, $P < 0.001$).

Seeley (1978) computed yearly survival as the product of winter and summer survival. Using the same approach, the combined expected yearly survival for 1993/1994 was 0.94 for established colonies and 0.55 for founder colonies. In the drought year of 1994/1995, the survival rate of established colonies was 0.59, and for founder colonies 0.083. The average over these two seasons was 0.76 for established colonies and 0.32 for founders.

The expected colony lifespan, L, can be computed from the summation (Seeley 1978):

$$L = 1 + \sum_{A=0}^{\infty} A[(f)(e)^{A-1}][1 - e]$$

where A is the age of colonies in years, f is the survival of founder colonies and e is the survival of established colonies. The expected colony lifespan of established colonies is given by (Seeley 1978):

$$L = 1 + \sum_{A=0}^{\infty} A[(e)^{A-1}][1 - e]$$

The expected lifespan of a founder colony in Wyperfeld is estimated to be 2.7 years, and for an established colony, 6.6 years. These figures may be low because of an exceptionally poor year in 1994/1995. Based on 1993/1994, a season of more typical rainfall, the expected survival of founder colonies is 10.2 years, and for established colonies, 17.6 years.

Survival of released swarms

The survival rate of the ten swarms released by us was low. Swarms were released on 2 November 1993 and were first re-inspected on 13 December 1993, when only three remained. This may be an underestimate of establishment because some swarms may have relocated. However, this seems unlikely, because mailing cages confine queens for about 48 h, and swarms are unlikely to leave after that period.

Of the ten introduced swarms, one survived until at least December 1993 (1 month), one to April 1994 (5 months), and one to at least April 1995 (17 months). The mean survival time of all introduced swarms was 73 ± 70 (SE) ($n = 10$) days, whereas the mean survival of natural swarms was 255 ± 46 days ($n = 23$). Natural swarms lived significantly longer than introduced swarms ($P = 0.011$, Mann-Whitney U test, 1 df). However, once established, our introduced swarms appeared to have typical survival rates. Because of the irregularity of sampling, and the very small number of released swarms available for analysis, these figures are very crude.

Re-colonisation of eradicated areas

Two colonies were killed at site 6 on 7 July 1993. No new swarms were found at site 6 during the experimental period. This was not due to an absence of bees near site 6. Foraging bees were seen in large numbers during most post-eradication surveys. Four colonies were killed at site 2 also on 7 July 1993. Two eradicated nest hollows at site 2 were found to be re-occupied by new swarms in December 1993. The possibility that these two colonies had survived treatment is extremely remote. The hollows had been carefully inspected in September 1993, and no flight activity was observed. During this early spring inspection, one hollow was beaten with a stick, which elicited no defensive response. The other hollow, at 15 m, was not beaten, but was observed for a protracted period though binoculars. These two new colonies were destroyed in April 1994. A third swarm that occupied a new nest site was noted in November 1994, and was immediately killed. The average re-occupation rate was therefore 15 colonies/km per year.

Discussion

In his detailed study of the demography and life history strategy of the feral bee population in upstate New York, Seeley (1978) concluded that honey-bee life history traits are characterised by low mortality, low reproductive rates, high population stability and iteroparity (repeated reproductions). The honey-bee population of Wyperfeld appears to have a capacity for higher reproductive rates and experiences quite high summer mortality. At Wyperfeld, the honey-bee population doubled between September 1993 and September 1994, and halved in the summer of 1994/1995 (Fig. 1), whereas in New York, the number of colonies was relatively stable. Interestingly, mortality is highest in summer at Wyperfeld, whereas in New York, most deaths occur in winter (Seeley 1978).

The densities of feral bee colonies at Wyperfeld exceed those previously reported for temperate areas (reviewed by Ratnieks et al. 1991) which range from 0.41 colonies/km^2 in Russia (Galton 1971) to 5.1 colonies/km^2 in Arizona (computed by Ratnieks et al. 1991 from Taber 1979). In tropical areas, densities are higher, in the region of 4.2 (McNally and Schneider 1996) to 8 colonies/km^2 (Ratnieks et al. 1991), but are still far less than those in Wyperfeld. However, bee nests in Wyperfeld are concentrated in the flood plains of Outlet Creek (which extend for about 1–2 km on either side), so our estimates do not reflect the density of bees over the whole area.

The number of feral colonies at Outlet Creek is higher than that which would be placed by bee-keepers if the area was available for commercial apiculture. Typically, in forest areas owned by the Department of Natural Resources and Environment, Bee Site Licences are issued at 3.2-km intervals. If we assume 130 colonies are typically sited at each apiary (B.P. Oldroyd, personal observations), then the density of commercial colonies is expected to be around 40 colonies/km^2.

Although not an independent study, these results tend to confirm our earlier observations that *A. mellifera* colonies in Wyperfeld National Park tend to have a clumped spatial distribution (Oldroyd et al. 1995). McNally and Schneider (1996) also reported a clumped spatial distribution for wild honey-bee colonies in Botswana. Colony aggregations could either arise by swarms being attracted to existing aggregations, or by short dispersal distances of swarms from the natal nest (Oldroyd et al. 1995; Schmidt 1995). Schmidt (1995) found the mean distance travelled by swarms in an environment replete with suitable nest boxes baited with Nasanov pheromones to be about 400 m, and has observed one swarm move less than 0.5 m. Seeley and Morse (1977) concluded that swarms "may prefer a nest site which is near the parent". On the other hand, many swarms move considerable distances from the natal nest (Schmidt 1995; Schneider 1995). A detailed genetic analysis of an aggregation over time would be useful in determining if existing aggregations attract new swarms, or if these aggregations arise through short dispersal distances.

Our data strongly suggest that the population of feral bees in Wyperfeld is self-sustaining and does not require migration of domestic swarms into the park for its maintenance. To maintain a stable population, the number of swarms per colony per year must equal:

$$\frac{1-e}{f}$$

For the average year of 1993/1994, each colony would need to produce just 0.11 swarms per season to maintain the population. For the drought year of 1994/1995, each established colony would need to produce 4.9 swarms per season. Using the combined survival estimates for the two years, established nests would need to produce 0.75 swarms each. These estimates are based on the assumption that there is little swarm mortality before they become founder colonies. If our released domestic swarms provide a fair indication of swarm mortality, seven out of ten swarms do not survive to become founder colonies. If we factor in 70% mortality of swarms before they found a nest, the population would be stable if each established nest produced 0.36 swarms per season based on 1993/1994 survivorship, 16.4 in 1994/1995, and 2.5 for the two seasons combined. Lee and Winston (1987) observed that established colonies produced an average of 2.2 swarms per season in British Colombia. Unmanaged colonies in Kansas produced 3.6 swarms per season. These data suggest that in an average season, the population of honey-bees at Wyperfeld would naturally increase because the number of swarms exceeds the required replacement rate, but in occasional drought years, it would decline precipitously. We conclude, therefore, that the population of feral bees in Wyperfeld National Park is firmly established.

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