EFFECTS OF CLIMATE ON PALAEARCTIC WARBLERS OVER-WINTERING IN INDIA

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(*With eleven text-figures*)

Human activities threaten many species with extinction worldwide. Migrant birds in Europe and North America include a number of well-studied examples of species undergoing contemporary population decline. In many cases, it is difficult to understand causes of the decline. We present results from a long-term population study of migrant warblers in India. We studied the Green Leaf Warbler *Phylloscopus nitidus* in Kalakad-Mundanthurai Tiger Reserve, south India over four winters (1992-96), and found significant effects of rainfall variation on population density and individual body condition. Winter rainfall affected both primary (leaf) and secondary (Arthropod) production, thereby affecting prey availability for the insectivorous warblers. These, in turn, were associated with differences in over-wintering persistence, body weight, and population density of the warblers. These effects were quite rapid, affecting densities within the first three months of the winter season. Records of long-term variation in rainfall suggest that warbler populations may fluctuate widely, even without overt changes to winter habitat. Such fluctuations make it difficult to detect declines due to other reasons, and also increase the risk of populations going extinct. Since most winter habitat appears to be saturated, we predict that any further loss of habitat will decrease the total population of the species.

Species extinction provides the most compelling evidence for the adverse environmental impact of humans. The evidence that many recent extinctions are indeed human driven comes from numerous case studies, which document the importance of introduced predators, parasites and competitors (e.g. Harris 1973, Hamann 1984, Savidge 1987, Pimm *et al.* 1955a, Steadman 1995), human hunting (e.g. the famous Passenger Pigeon, Blockstein and Tordoff 1985; many island species, Steadman 1995), and habitat loss through clearing for agriculture and timber (e.g. Terborgh 1989, Reichel *et al.* 1992, Rappole 1995, Steadman 1995). Such studies are augmented by estimates of the background rate of extinction, as obtained from the fossil record (Jablonski 1995). They show that we can expect an extinction spasm in the next century larger than any since the Cretaceous (*c.* 65 million years ago, Jablonski 1995, Pimm *et al.* 1995b). For birds, the rate of extinction is certainly higher now than it has ever been. Steadman (1995) presents zooarcheological evidence suggesting that as many as 2000 bird species — about 15% of the number of species present today (Sibley and Monroe 1990) — have gone extinct in the islands of the tropical Pacific, since humans first colonized the islands. The only plausible explanation for the increased rates of extinction is the presence of humans.

While case studies of extinction provide an important focus for conservation science, they are also a little frustrating for the conservationist, whose main aim is to preserve extant species. On the other hand, studies of declining populations, while providing information about the impact of a changing environment, also allow us the luxury of trying to reverse the decline.

A serious difficulty in the study of population declines is that, unlike the case of extinctions, we have no good estimates of natural population fluctuations before human intervention. It is clear that climate fluctuations can have a large impact, e.g. droughts causing heavy mortality (Gibbs and Grant 1987, Baillie and Peach 1992, Blake *et al.* 1992). There have been major changes in the geographical range for many species in Britain this century attributable to relatively minor climatic changes (Burton 1995). Over the past 2 million years, ice ages have caused extreme climatic changes which

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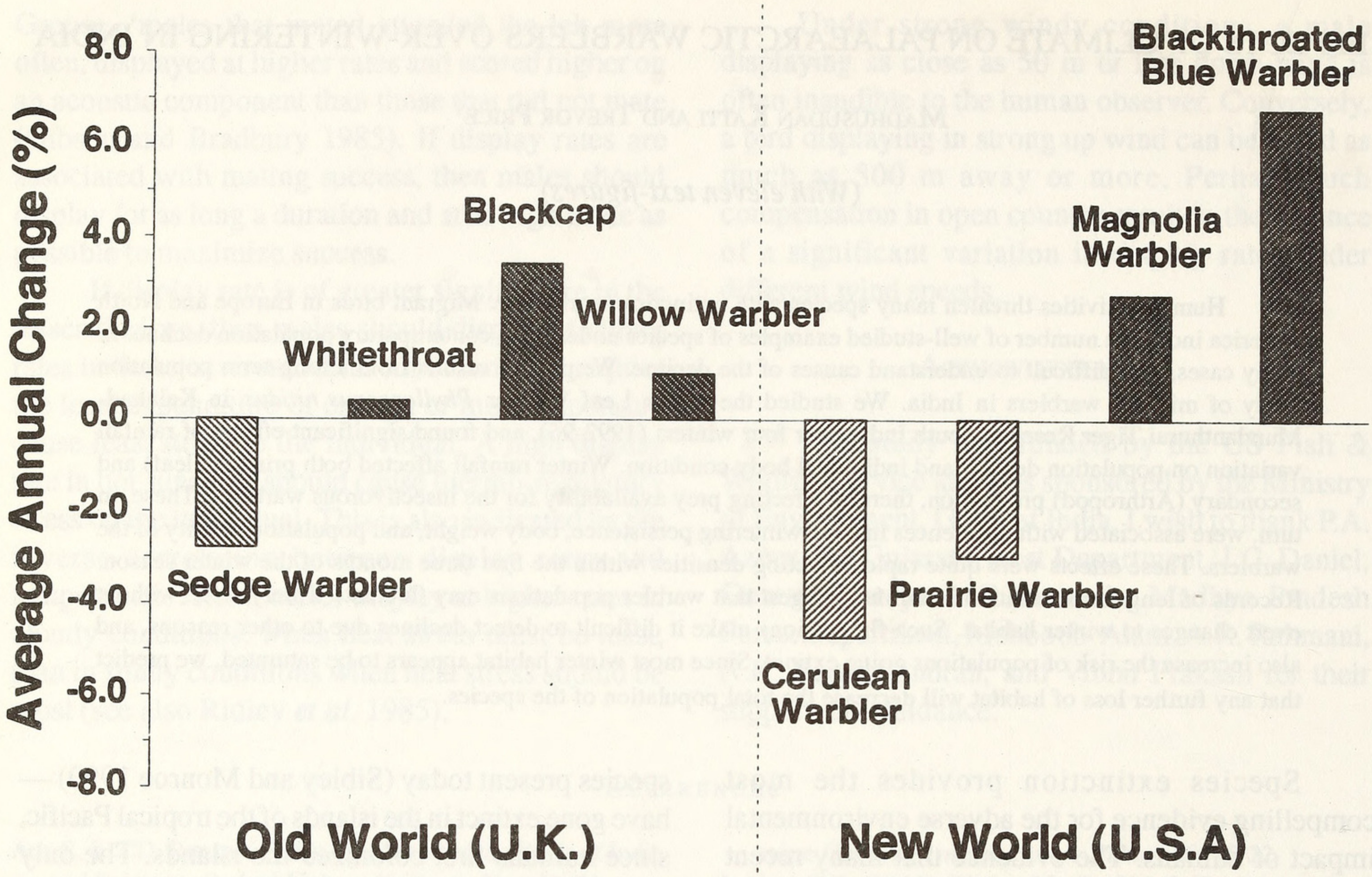

Fig. 1. Average annual changes (%) in several warbler species in Europe and North America in recent decades. Data for U.K. are from Baillie and Peach (1992), using British Trust for Ornithology (BTO) data for 1964-1989, while those for U.S.A. are from James *et al.* (1996), using Breeding Bird Survey (BBS) data for 1966-1992.

must have had an enormous impact on population sizes.

In this paper we evaluate the impact of climate — specifically winter rainfall — on population sizes of over-wintering migrant Palaearctic warblers in India, as a means by which to evaluate the non-human factors that can cause population fluctuations. We chose to focus on warblers because they have been well studied in Europe and North America, and have become a classic example of species in decline (Terborgh 1989, Hagan and Johnston 1992, Rappole 1995). Habitat loss has been implicated as a cause of decline for some specific case studies (Rappole 1995), but some outstanding questions remain. Firstly, not all species are declining (Fig. 1, Baillie and Peach 1992, James *et al.* 1996). Secondly, even for those species which are declining it can be difficult to detect a root cause, which may be on the breeding grounds, on the wintering grounds, or during migration (Böhning-Gaese 1992, Sherry and Holmes 1992, 1996, Böhning-Gaese *et al.* 1993). Third, a role for habitat loss has been difficult to demonstrate (Rappole and McDonald 1994, Rappole 1995, Sherry and Holmes 1996). These questions make it imperative to understand the impact of climate on population sizes.

We report results of a four-year study on the Green Leaf Warbler, *Phylloscopus nitidus*, on its wintering grounds. This species over-winters in south India, and breeds in the Caucasus (> 5000 km away, Cramp 1992). We studied the population over-wintering on Mundanthurai plateau in the Kalakad-Mundanthurai Tiger Reserve in the southern Western Ghats from December 1992 to January 1996. The prime purpose of this paper is to demonstrate a connection between rainfall and over-winter

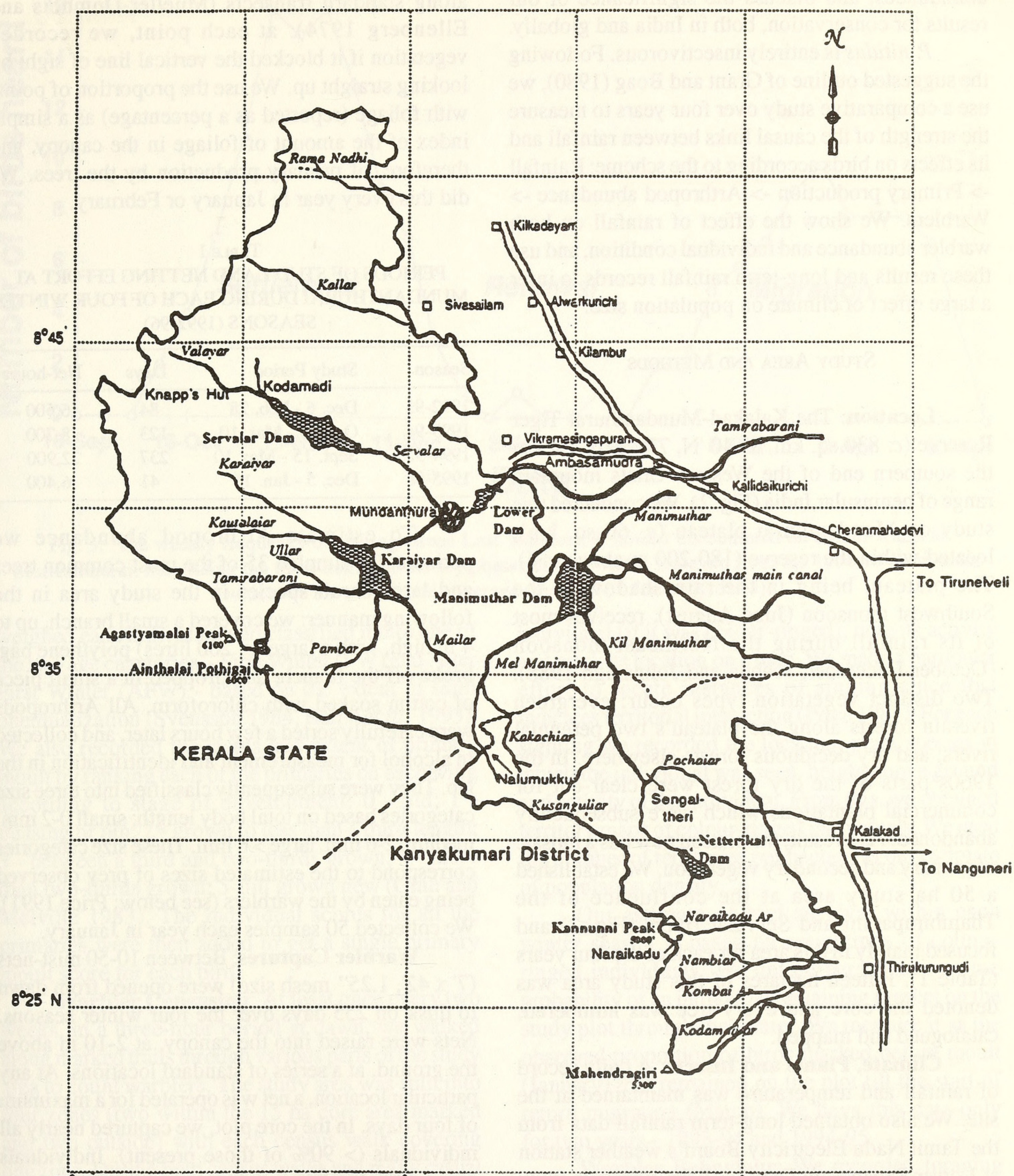

Fig. 2. Location of study area in Kalakad-Mundanthurai Tiger Reserve, Tamil Nadu.

abundances, and discuss the significance of our results for conservation, both in India and globally.

P. nitidus is entirely insectivorous. Following the suggested outline of Grant and Boag (1980), we use a comparative study over four years to measure the strength of the causal links between rainfall and its effects on birds according to the scheme: Rainfall -> Primary production -> Arthropod abundance -> Warblers. We show the effect of rainfall on both warbler abundance and individual condition, and use these results and long-term rainfall records to infer a large effect of climate on population size.

Study Area and Methods

Location: The Kalakad-Mundanthurai Tiger Reserve (*c.* 830 sq. km, 8° 40 'N, 77° 20 'E) lies at the southern end of the Western Ghats mountain range of peninsular India (Fig. 2). We conducted this study on Mundanthurai plateau (*c.* 60 sq. km), located within the reserve (180-200 m above msl). The plateau, being in the rain shadow of the Southwest monsoon (June-August), receives most of its rainfall during the Northeast monsoon (October-December, Joshua and Johnsingh 1988). Two distinct vegetation types occur: evergreen riverain forests along the plateau's two perennial rivers, and dry deciduous forests elsewhere. In the 1960s parts of the dry forest were clear-cut for commercial plantations which were subsequently abandoned. As a result, the plateau now has a mosaic of primary and secondary vegetation. We established a 50 ha study area at the confluence of the Thambiraparani and Servalar rivers (Fig. 2) and focused mainly in this area for each of the four years (Table 1). Fifteen hectares of this study area was denoted the core and every tree was numbered, catalogued and mapped.

Climate, Plants and Insects: A daily record of rainfall and temperature was maintained at the site. We also obtained long-term rainfall data from the Tamil Nadu Electricity Board's weather station at Lower Papanasam Dam, *c.* 3 km from our study area (Fig. 2). One of us (M. Katti) also recorded plant phenology by estimating tree cover at 200 points along standard transects (Mueller-Dombois and Ellenberg 1974): at each point, we recorded vegetation if it blocked the vertical line of sight by looking straight up. We use the proportion of points with foliage (reported as a percentage) as a simple index of the amount of foliage in the canopy, and therefore, of primary production by the trees. We did this every year in January or February.

Table 1
PERIODS OF STUDY AND NETTING EFFORT AT MUNDANTHURAI DURING EACH OF FOUR WINTER SEASONS (1992-96)

Season	Study Period	Days	Net-hours
1992-93	Dec. 6 - Feb. 28	84	6,500
1993-94	Oct. 10 - Mar. 10	123	8,700
1994-95	Sept. 15 - May 10	237	22,900
1995-96	Dec. 5 - Jan. 15	41	6,400

To estimate Arthropod abundance we periodically sampled 35 of the most common trees and large shrub species in the study area in the following manner: we covered a small branch, up to 4 m high, with a large (*c.* 200 litres) polythene bag, broke off the branch, and dropped in a small piece of cotton soaked with chloroform. All Arthropods were carefully sorted a few hours later, and collected in alcohol for measurement and identification in the lab. They were subsequently classified into three size categories based on total body length: small 0-2 mm, medium 2-6 mm, large > 6 mm. These size categories correspond to the estimated sizes of prey observed being eaten by the warblers (see below; Price 1991). We collected 50 samples each year in January.

Warbler Captures: Between 10-50 mist-nets (7' x 42', 1.25" mesh size) were opened from dawn to dusk on 255 days over the four winter seasons. Nets were raised into the canopy, at 2-10 m above the ground, at a series of standard locations. At any particular location, a net was operated for a maximum of four days. In the core plot, we captured nearly all individuals (> 90% of those present). Individuals were ringed using a unique combination of one numbered aluminium ring from the Bombay Natural History Society and up to two colour rings. We

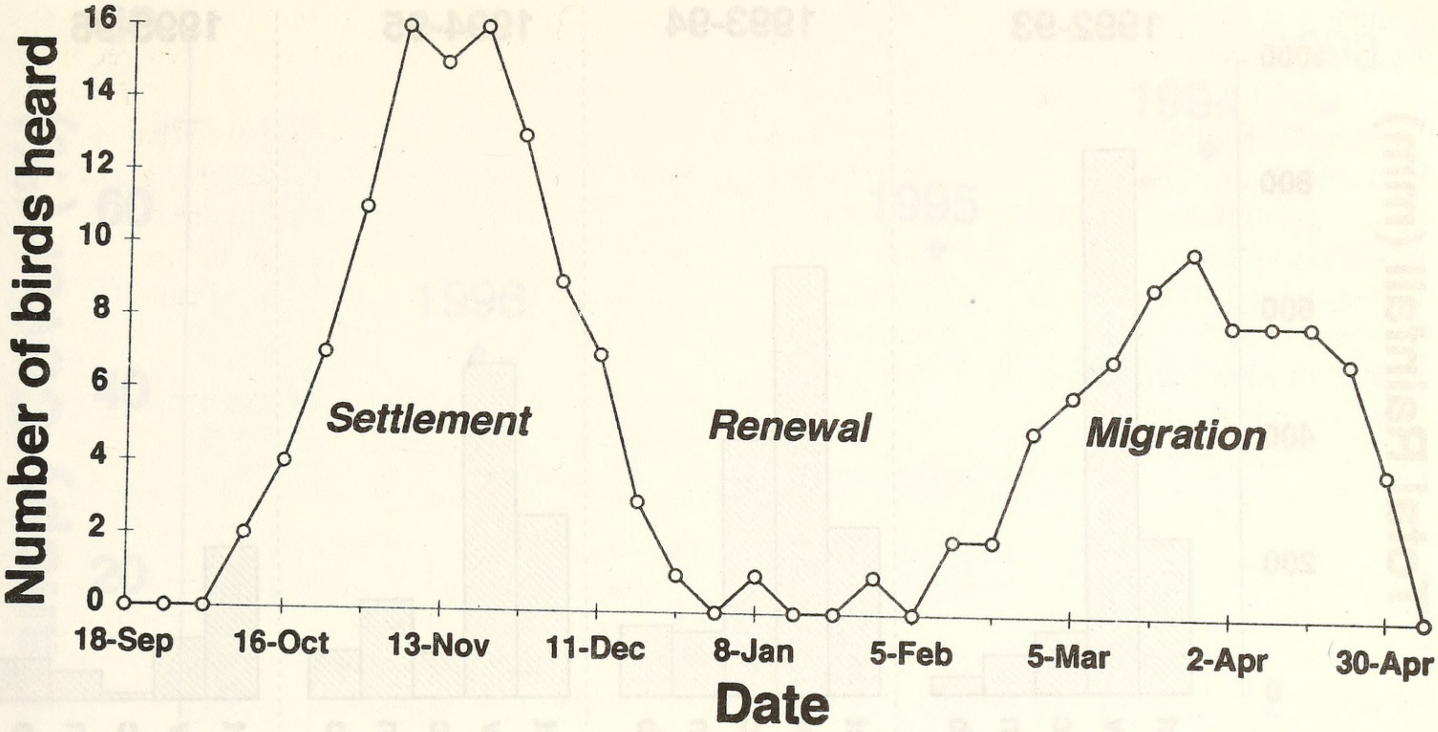

Fig. 3. The weekly frequency of singing Green Leaf Warblers, *P. nitidus* encountered on census walks at Mundanthurai, illustrating the three main life-history phases during winter. Data are from the 1994-95 season, for which we have complete coverage (see Table 1 for study dates).

weighed each individual and classified it into one of the two age categories - First Winter (FW) and After First Winter (AFW) - based on the extent of skull pneumatization (Svensson 1984, Ralph *et al.* 1993). We also recorded the status and extent of primary moult by ranking each of the primaries on each wing according to stage of development: 0 - old; 1 - missing or pin; 2 - grown to less than a third length; 3 - between a third and two-thirds grown; 4 - more than two-thirds grown; 5-full grown new (Ginn and Melville 1983). The individual scores for all the primaries were then added to get a single primary moult score for each bird.

Warbler Censusing: At least once every two weeks, in a three-hour period at dawn, we walked along marked trails through various parts of the study area to count warblers. The study area was split into four zones (two within the 15 ha core area marked and two outside) with each census walk covering one zone. During both census walks and many casual observations, every time a *P. nitidus* was heard calling, we attempted to locate and identify the individual (if it was colour-ringed), note its activity and mark its location on a map. We made a particular effort to locate instances of singing since that indicates territorial interaction (Price 1981). For each sighting we recorded the location, plant species in which the individual was seen, height above ground and activity of the individual. From this, we obtained territory maps of colour-ringed individuals. We used the number of territories per hectare as our estimate of population density.

Our estimate of bird survival within each winter season is based on resightings of colour-ringed individuals. We define persistence as the probability of an individual remaining present on the study plot through the winter. We measure it as the observed proportion of birds marked before moult (January) that remained on the plot till the start of return migration (March). We have this data only for two years - 1993-94 and 1994-95.

Warbler Behaviour: We recorded foraging and other behaviour in two ways. Individuals were observed until they made the first feeding movement:

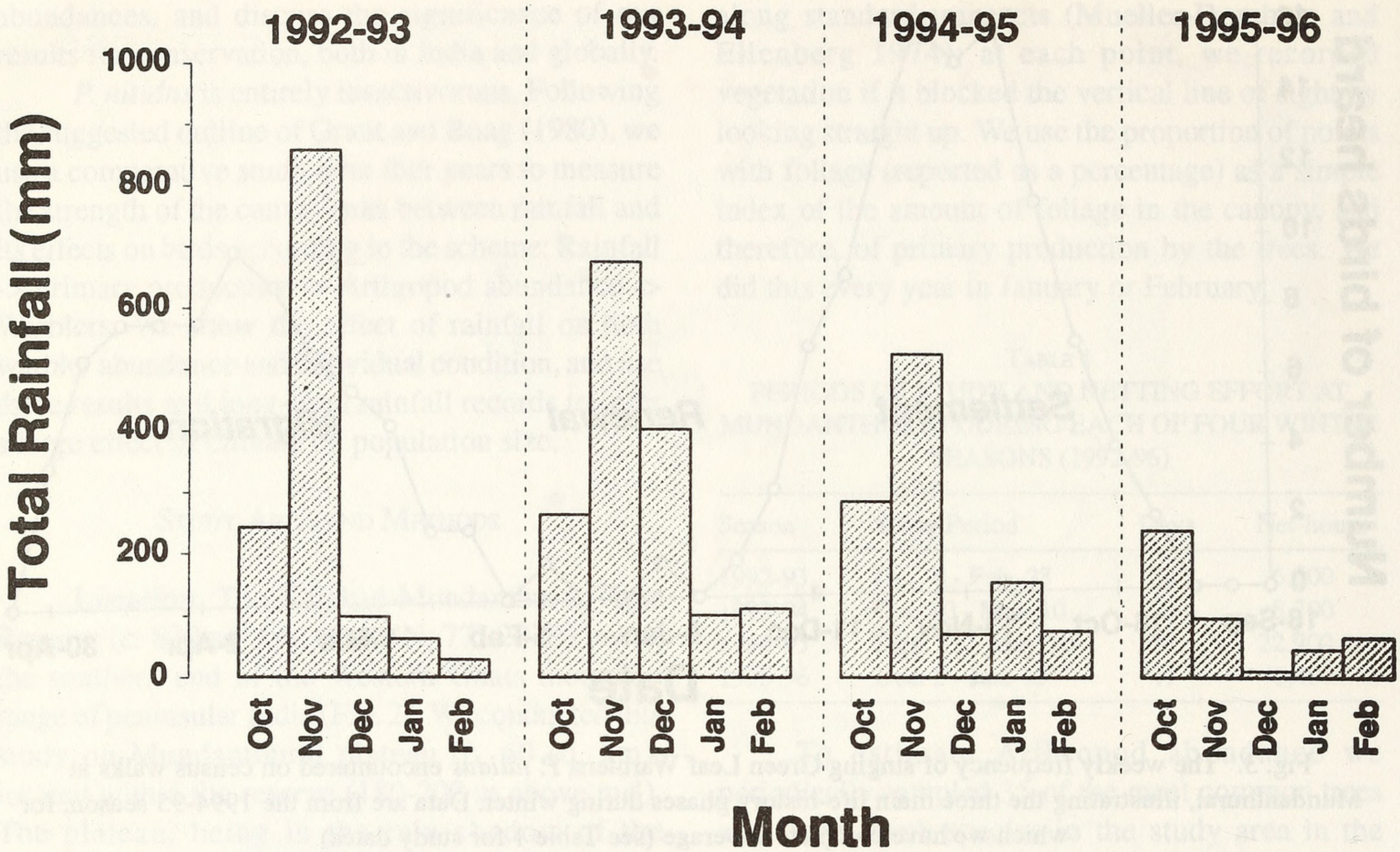

Fig. 4. Winter rainfall (mm) in Mundanthurai over the past four winters (1992-1996).

the type of movement, its location, and an estimate of prey size were recorded, following Price (1991). This method ensures independence of each observation. We use it to estimate the distribution of prey sizes eaten. Price (1991) showed a high correlation across species between this measure and prey size as measured from the faeces. In addition, we followed focal individuals for as long as possible (up to 30 minutes), recording all foraging attempts and other behaviour into a hand held tape recorder. This provided data on foraging rates.

Results

Natural History: *P. nitidus* first arrives in northern India during August (Gaston 1981), and takes over a month to reach southern India. At Mundanthurai, arrival usually begins near the end of September, and continues through early December (Fig. 3). Individuals are solitary and territorial in the winter, with both sexes holding independent territories throughout the winter. In Mundanthurai, settlement usually begins along the riverain gallery forest, which is more evergreen, and has considerably more foliage in September (at the end of a long dry season, see below). Birds arriving later occupy areas of deciduous forest away from the river. All birds which return from previous years retain their old territories in both habitats (see also Price 1981). This suggests strong site fidelity as well as consistency in timing, for previous territory holders in the deciduous forests arrived later than those in the riverain forest.

In Mundanthurai, the *P. nitidus* population exhibits three distinct phases (illustrated in Fig. 3): The first phase, settlement, runs from late September to December, and comprises arrival, habitat selection and territory establishment. About 30% of birds caught during arrival underwent a partial moult of their primary coverts and some body feathers either during migration or immediately upon arrival. It is characterized by frequent interactions among

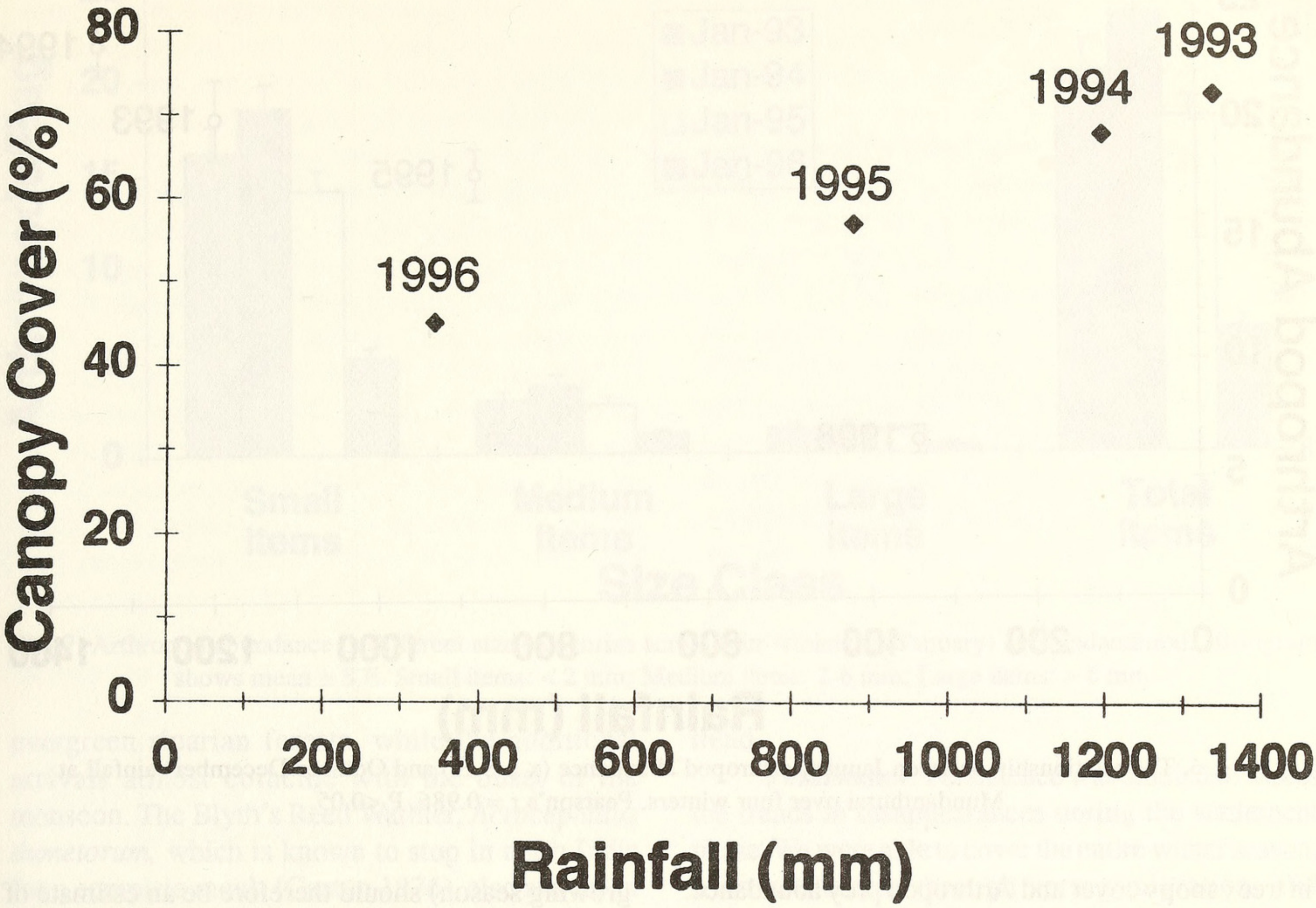

Fig. 5. The relationship between January canopy cover and October-December rainfall at Mundanthurai over four winters (1992-1996). Pearson's r = 0.993, $P < 0.05$.

individuals while territory boundaries are negotiated (Fig. 3). Territorial behaviour ranges from simple calling through intense face-to-face contests lasting several hours (apart from breaks during foraging bouts), and sometimes continuing over many weeks. During such interactions, birds chase each other, flick their wings and often sing continuously. Singing is seldom heard outside of such contests, and both sexes sing. Many individuals disappear (permanently) during this period, after failing to obtain territories.

The second phase, which we call the renewal phase, lasts from January to mid-March, when the birds undergo a complete moult. This is socially the quietest part of the season, with very little interaction among individuals, and rates of calling are at the lowest (Fig. 3). A moult of all feathers starts near the end of the Northeast monsoon in January and lasts through February, often extending into late March. During moult, most individuals drop most of their flight feathers at once and become virtually flightless for up to two weeks.

The final phase, migration, begins soon after the end of moult, by mid-March, and lasts until late April when all the birds disappear. During this phase foraging rates increase as individuals start accumulating fat in preparation for the return migration. Some migrating birds, presumably from more southern areas, pass through Mundanthurai, mainly along the rivers, and there is an increase in the rates of vocalization and interaction.

While the population conforms to the above pattern of life-history during each winter, we found considerable year-to-year variation in measures of individual condition, and in population parameters. Much of this variation appears to be driven by fluctuations in winter rainfall, and associated changes

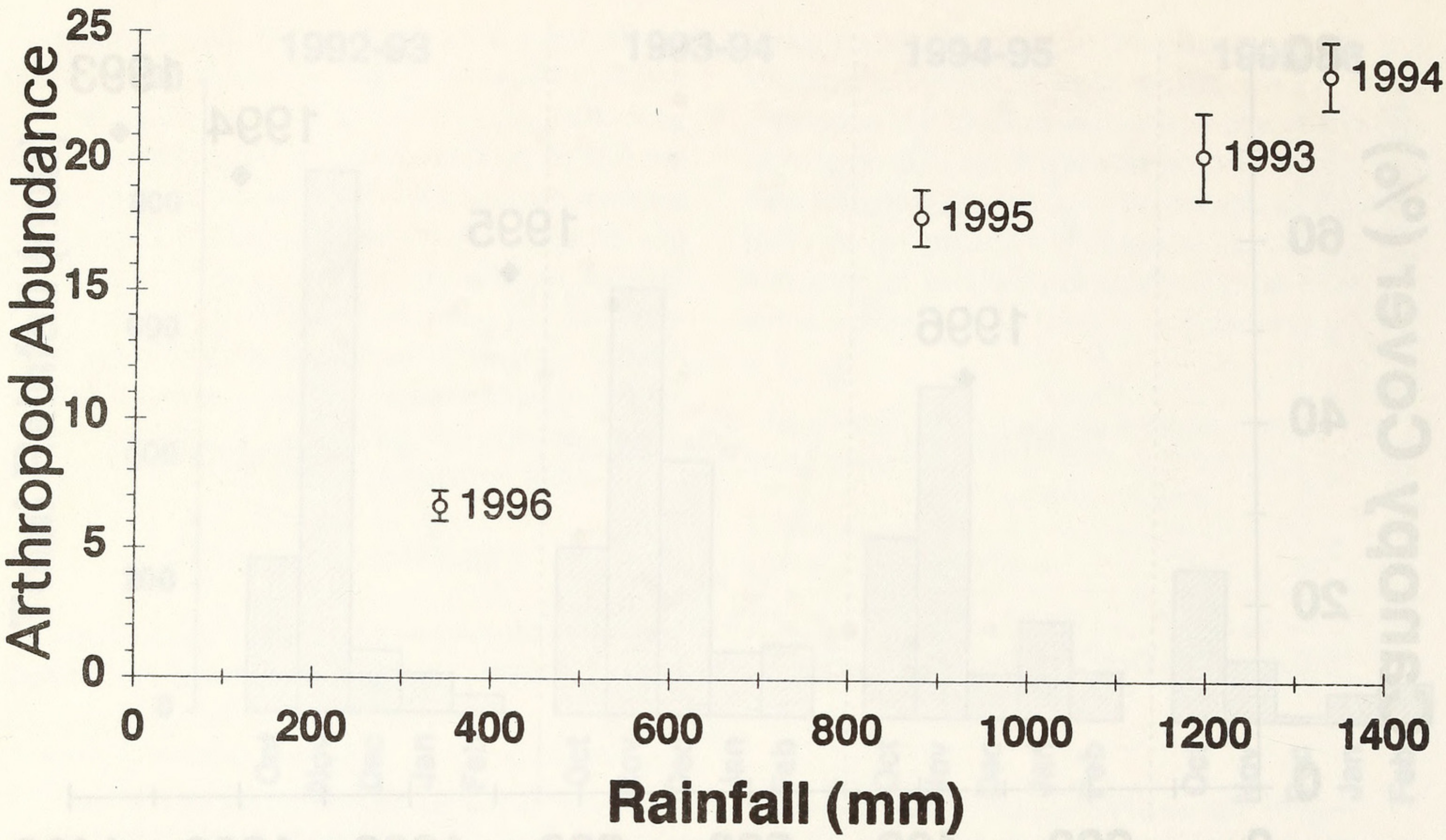

Fig. 6. The relationship between January arthropod abundance (x ± S.E.) and October-December rainfall at Mundanthurai over four winters, Pearson's r = 0.986, P <0.05.

in tree canopy cover and Arthropod prey abundance. We describe the trends in each of these variables below and look at their relationship to warbler abundance and individual condition.

Rainfall: During the study, Mundanthurai experienced three-fold variation in winter (October-February) rainfall, with high rainfall in the first two winters, to near-drought in 1995-1996 (Fig. 4). The fluctuation is similar to that in the past (1960-1985, Fig. 11), though the first two years (1992 and 1993) were wetter than any between 1960-1985.

Plant Phenology: Mundanthurai, which is in the rain shadow for the Southwest monsoon, experiences a long dry season between March and September, when most of the plateau's forest is leafless, except some evergreen species along the rivers. The main leaf flush, and season of primary productivity, starts with the Northeast monsoon, arriving usually in November. Our estimate of tree canopy cover in Jan./Feb. (at the end of the monsoon growing season) should therefore be an estimate of leaf cover at its peak. The estimate varied considerably across years (Coefficient of Variation = 20.5%, N = 4) and showed a strong positive correlation with October-December rainfall (Fig. 5, Pearson's r = 0.99, P < 0.05, N = 4).

Arthropods: Arthropod abundance follows the first leaf flush in late November (M. Katti and T. Price, unpublished data). Our estimate of total Arthropod abundance, also measured in January, near the end of the growing season, was strongly positively correlated with October-December rainfall (Fig. 6, Pearson's r = 0.99, P < 0.05, N = 4), and with canopy cover (Pearson's r = 0.96, P < 0.05, N = 4). In the driest year, total Arthropod abundance was 28% of that in the wettest year. Similarly, large prey in the driest year was 29% of that in the wettest year comparison, and Arthropod abundance showed a parallel trend in all three size categories (Fig. 7).

Warbler Density: As described earlier, the early arriving warblers of October occupy the semi-

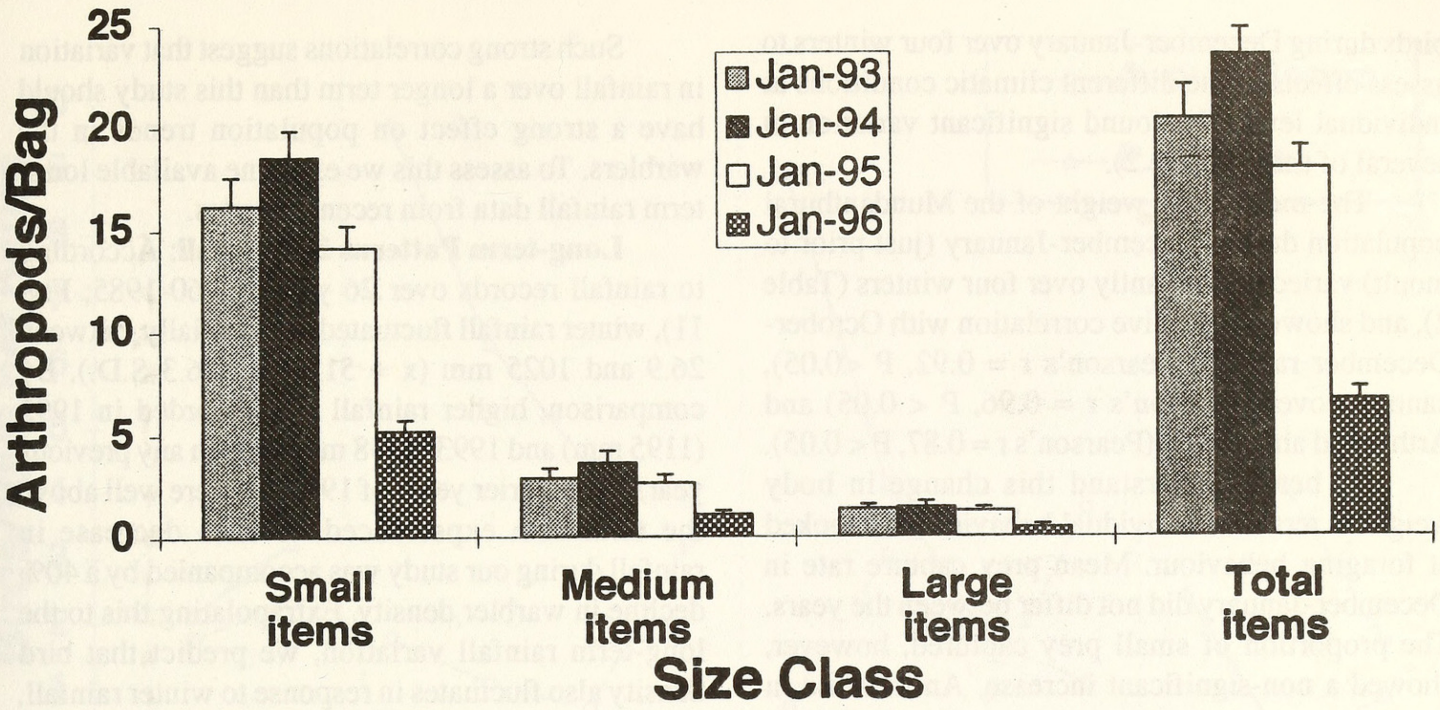

Fig. 7. Arthropod abundance in different size categories across four winters (in January) at Mundanthurai. Histogram shows mean ± S.E. Small items: < 2 mm; Medium items: 2-6 mm; Large items: > 6 mm.

evergreen riparian forests, while the additional arrivals almost coincide with the onset of the monsoon. The Blyth's Reed Warbler, *Acrocephalus dumetorum*, which is known to stop in north India for a complete moult (Gaston 1976), also arrives in Mundanthurai with the Northeast monsoon. Gaston (1981) reported that some Greenish Warblers, *P. trochiloides*, lingered in his study area in Delhi for a few days during passage, before disappearing. We speculate that individuals arriving late in Mundanthurai stop at other locations enroute, possibly tracking local resource abundances (like some African wintering species, Marchant 1992, Hedenström *et al.* 1993). Arrivals peak during early December and densities stabilize by the end of December, once territories have been established. The number of territories on the core plot during our study differed between the four years (Table 2). Density in January 1996 (1.9 birds/ha) was about 60% of that in January 1993 (3.2 birds/ha). A similar trend is apparent in a comparison of mist-net capture rates for *P. nitidus* over four years (Fig. 8) - note that there is considerable variation in capture rate within each season; the appropriate comparison is for each month between years, which shows the declining trend.

Persistence: Persistence was studied to assess the trends in disappearances during the settlement phase. We were able to cover the entire winter season, from settlement through spring migration, and estimate persistence, for only two years (1993-94 and 1994-95). Comparing the fate of birds captured during October 15-December 31 in these two years, we found an almost two-fold difference in persistence (Fig. 9, X^2 test, $P < 0.01$). The trend is the same as that in density – the drier year (1994-95) had lower persistence than the wetter year (1993-94).

Effects on Individuals: We have shown a correlation between environment and population density. Such environmental influences may also affect the fitness of surviving individuals, since body condition at the end of winter is likely to influence the ability to migrate and breed successfully. Price (1981) found that during the dry season in the Eastern Ghats (which is in the middle of the winter there) mean body weight of Greenish Warblers, *P. trochiloides*, decreased. This was also the time when birds with small territories disappeared (which was equated with death, Price 1981). We compared morphological and behavioural traits of persisting birds during December-January over four winters to assess effects of the different climatic conditions at individual level. We found significant variation in several of them (Table 2).

The mean body weight of the Mundanthurai population during December-January (just prior to moult) varied significantly over four winters (Table 2), and showed a positive correlation with October-December rainfall (Pearson's $r = 0.92$, $P < 0.05$), canopy cover (Pearson's $r = 0.96$, $P < 0.05$) and Arthropod abundance (Pearson's $r = 0.87$, $P < 0.05$).

To better understand this change in body weight in terms of individual behaviour, we looked at foraging behaviour. Mean prey capture rate in December-January did not differ between the years. The proportion of small prey captured, however, showed a non-significant increase. An increase in the proportion of small items might be expected with a decrease in the availability of food (Fig. 7), and if real, suggests a lower Arthropod biomass intake in the drier years.

While food availability in January might affect the immediate probability of survival, its apparent effects on body condition could also have repercussions on migrating ability and breeding success. This is illustrated through our comparative study of primary moult over four years. We found that the onset of primary moult — estimated as the x-intercept of the regression of primary moult on date — was delayed during years of low rainfall (Fig. 10). Since studies in the breeding season have found late-arriving birds to have lower breeding success (Price *et al.* 1988, Price and Jamdar 1990), we predict lower breeding success in the summers following the drier winters.

We can now hypothesize causal links between rainfall, canopy cover, arthropod abundance and warbler abundance. All of these variables are strongly and significantly, correlated (Table 3). The hypothetical causal pathway underlying these correlations may be illustrated as follows (with the correlation values shown above each path):

$r = 0.993$ $r = 0.962$ $r = 0.97$

Rainfall ⟶ Canopy Cover ⟶ Arthropod Abundance ⟶ Warbler Density

Such strong correlations suggest that variation in rainfall over a longer term than this study should have a strong effect on population trends in the warblers. To assess this we examine available long-term rainfall data from recent decades.

Long-term Patterns in Rainfall: According to rainfall records over 26 years (1960-1985; Fig. 11), winter rainfall fluctuated substantially, between 26.9 and 1025 mm ($x = 512.1 \pm 326.3$ S.D.). By comparison, higher rainfall was recorded in 1992 (1195 mm) and 1993 (1338 mm) than in any previous year, but the drier years of 1994-95 were well above the minimum experienced. A 75% decrease in rainfall during our study was accompanied by a 40% decline in warbler density. Extrapolating this to the long-term rainfall variation, we predict that bird density also fluctuates in response to winter rainfall.

Climatic factors such as rainfall variation are likely to have general effects on all bird species in

TABLE 2

SOME CHARACTERISTICS OF THE GREEN LEAF WARBLER *Phylloscopus nitidus* ON MUNDANTHURAI PLATEAU OVER FOUR WINTERS (1992-96)

	1992-93	1993-94	1994-95	1995-96
Body Weight[1]	7.6 ± 0.1	7.7 ± 0.1	7.5 ± 0.1	7.3 ± 0.1
Onset of Moult[2]	Jan.-9	Jan.-5	Jan.-23	>Jan.-15
Prey Capture Rate[3] (per min., Dec./Jan.)	0.7 ± 0.2	0.7 ± 0.1	0.8 ± 0.2	0.6 ± 0.4
Proportion of small items in prey (%)[4]	80	83	86	91
Density[5] (territories/ha)	3.2	3.1	2.8	1.9

1. $\bar{x} \pm$ s.e., n = 12 (1992-93), 20 (1993-94), 17 (1994-95), 11 (1995-96), ANOVA, F-ratio = 3.9, $P < 0.05$.
2. Onset of moult is estimated from regression of primary moult score on date.
3. $\bar{x} \pm$ s.e., n (minutes) = 35 (1992-93); 41 (1993-94); 50 (1994-95); 38 (1995-96).
4. From point observations of foraging; n = 56 (1992-93); 100 (1993-94); 112 (1994-95); 86 (1995-96).
5. From territories mapped on 15 ha core plot.

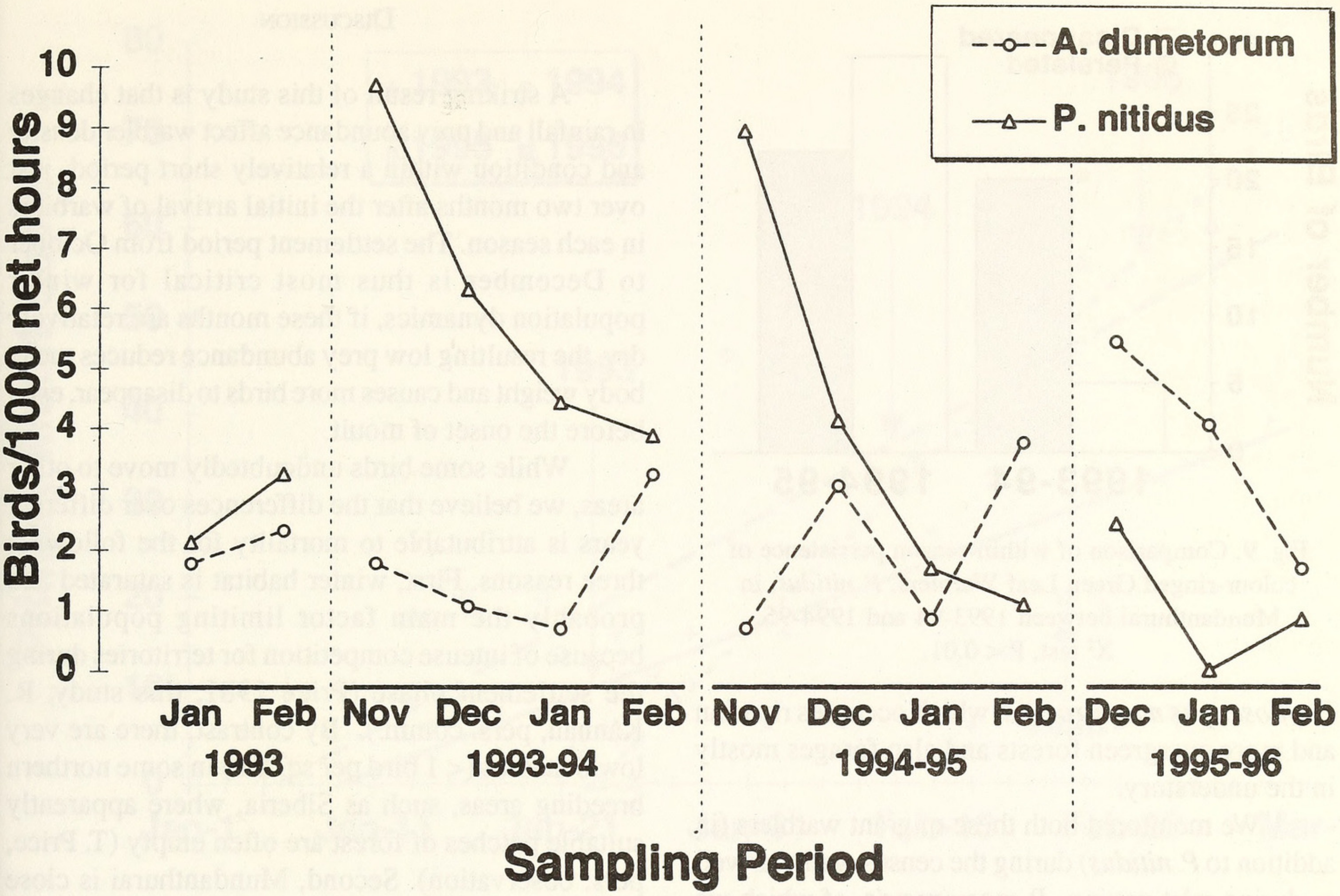

Fig.8. Monthly capture rates (birds per 1000 net-hours) for Green Leaf Warbler, *Phylloscopus nitidus* and Blyth's Reed Warbler, *Acrocephalus dumetorum* at Mundanthurai during four winters (1992-1996).

TABLE 3
MATRIX OF CORRELATIONS BETWEEN RAINFALL, CANOPY COVER, ARTHROPOD ABUNDANCE AND WARBLER DENSITY OF MUNDANTHURAI, USING DATA FROM FOUR YEARS (1992-96). ALL VALUES ARE PEARSON'S 'r'

	Rainfall October-December	Canopy Cover (%)	Arthropod Abundance
Canopy Cover (%)	0.993	—	—
Arthropod Abundance	0.986	0.962	—
Green Leaf Warblers (territories per ha)	0.969	0.939	0.970

an area. Having elaborated on one species in detail, we now look at our (less intensive) data on other migrant warblers wintering in Mundanthurai, and find parallel trends.

Other species: *P. nitidus* dominates the guild of foliage-gleaning insectivores in the forest canopy, and is perhaps the only one to maintain an entirely insectivorous diet through the winter. Other resident sympatric canopy foliage-gleaners include the Iora, *Aegithina tiphia,* which also feeds on fruit and nectar, Sunbirds (two species of *Nectarinia*) and Flowerpeckers (two species of *Dicaeum*) which are partial nectar-feeders and Minivets (two species of *Pericrocotus*) which are not very common. We did not measure the abundance of these species. The most common insectivore in the forest understory is another Palearctic migrant Sylviid warbler, the Blyth's Reed Warbler *Acrocephalus dumetorum,* which also overlaps with *P. nitidus* in their breeding range. A third common migrant warbler is the Himalayan breeding Large-billed Leaf Warbler

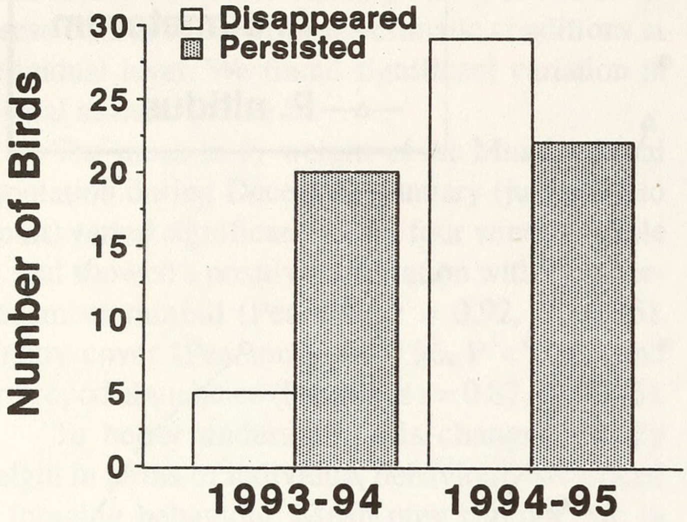

Fig. 9. Comparison of within-season persistence of colour-ringed Green Leaf Warblers, *P. nitidus*, in Mundanthurai between 1993-94 and 1994-95. X^2 test, $P < 0.01$.

Phylloscopus magnirostris, which occupies riparian and more evergreen forests and also forages mostly in the understory.

We monitored both these migrant warblers (in addition to *P. nitidus*) during the census walks as well as during mist-netting. *P. magnirostris,* of which we mapped territories also, shows similar trends as *P. nitidus* in density; the riverain stretches of the study plot (< 2 ha) had 5 territories in 1992-93 and 1993-94, 3 territories in 1994-95 and 2 territories in 1995-96. *A. dumetorum* is harder to observe due to its preference for foraging in the interior of dense bushes, so we were not able to identify individuals for accurate territory mapping. The mist-netting data, however, show an interesting trend (Fig. 8): *A. dumetorum* capture rates tend to be negatively correlated with *P. nitidus* capture rates ($r = 0.47$, $N = 4$, not significant), and more *A. dumetorum* were caught in the driest year than in other years. Since the nets are placed up in the canopy, mostly above the foraging range of *A. dumetorum,* these capture rate data may be interpreted as an index of the relative frequency of canopy foraging by *A. dumetorum.* Thus we do not attribute the change in capture rate to change in densities, but rather to change in foraging in response to low food availability (see also Price 1981).

Discussion

A striking result of this study is that changes in rainfall and prey abundance affect warbler density and condition within a relatively short period, just over two months after the initial arrival of warblers in each season. The settlement period from October to December is thus most critical for winter population dynamics, if these months are relatively dry, the resulting low prey abundance reduces mean body weight and causes more birds to disappear, even before the onset of moult.

While some birds undoubtedly move to other areas, we believe that the differences over different years is attributable to mortality for the following three reasons. First, winter habitat is saturated and probably the main factor limiting populations because of intense competition for territories during the settlement phase (Price 1981, this study, R. Kannan, pers. comm.). By contrast, there are very low densities (< 1 bird per sq. km) in some northern breeding areas, such as Siberia, where apparently suitable patches of forest are often empty (T. Price, pers. observation). Second, Mundanthurai is close to the species' southern range limit within peninsular India, and arrival here is also fairly late (more than two months after birds start leaving the breeding area: Cramp 1992). Birds failing to obtain territories here do not have much space, time, or energy reserves (arriving birds have virtually no visible subcutaneous fat left; M. Katti, unpublished data) to explore other areas. Finally, rainfall across the eastern half of peninsular India is largely under the influence of the Northeast monsoon currents and a lower amount of winter rainfall in Mundanthurai represents general failure of the monsoon. Any dispersing warblers are thus unlikely to find conditions different from Mundanthurai elsewhere during dry years.

We have shown that the reduction in prey abundance in dry years correlates with lower densities and also with lower body weight by January, indicating that surviving birds are in poorer physiological condition. An immediate consequence of this is on the timing of moult. It is known that moult — particularly of flight feathers — is

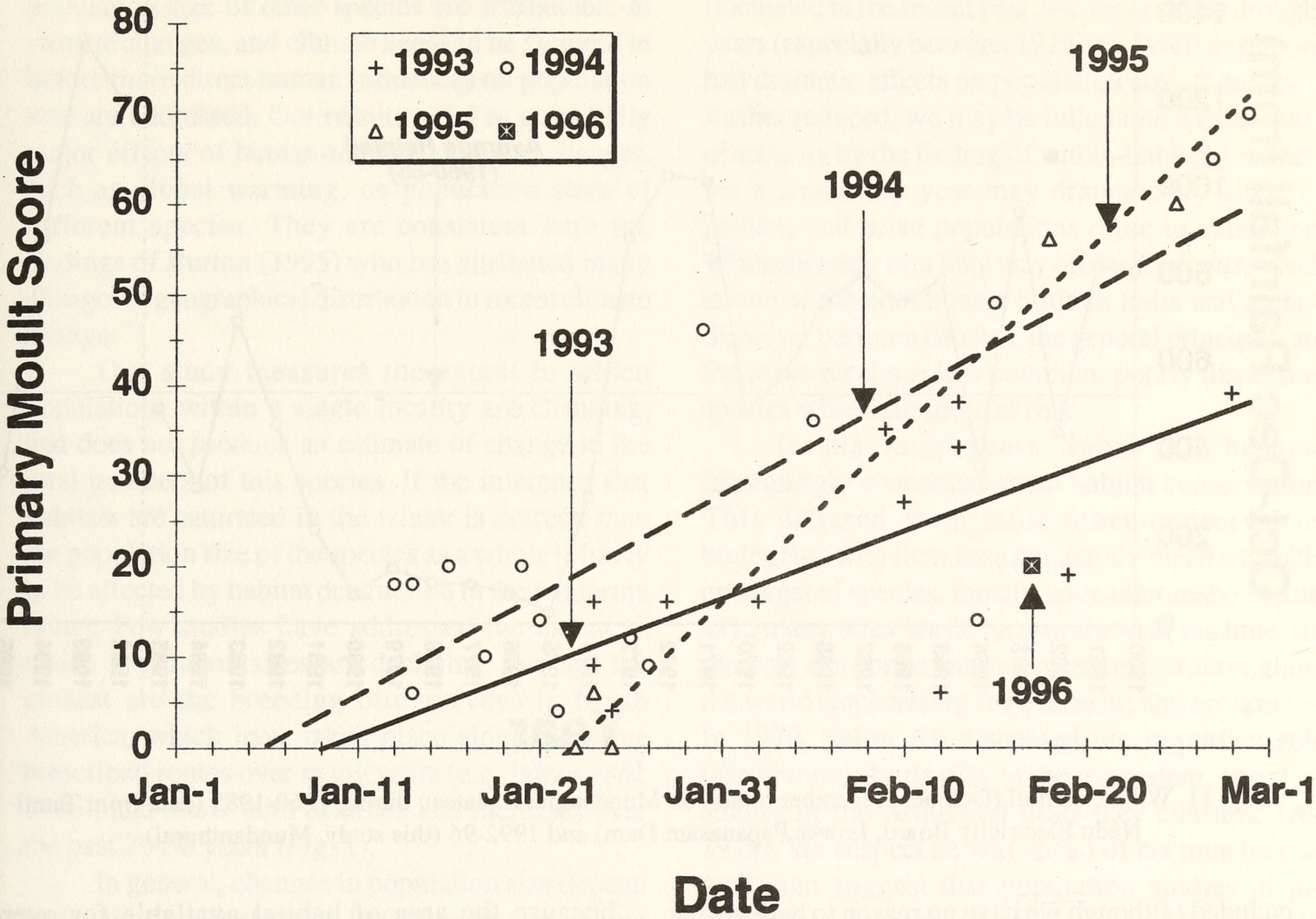

Fig. 10. The relationship between primary moult score and date for the Green Leaf Warbler, *P. nitidus*, at Mundanthurai, 1994-1996. Only one bird was captured during moult in 1996. Regression, $P < 0.05$ for all three years 1993, 1994, 1995; ANCOVA, Moult vs. Date, Year: whole model, F-ratio = 16.42, $P < 0.01$; date(*) year interaction, F-ratio = 3.95, $P < 0.05$.

physiologically stressful and increases the risk of predation as birds lose their flight efficiency (Bensch *et al.* 1991, Gosler 1991, Lindström *et al.* 1993). At the same time, every bird must complete its moult in order to be able to fly back to the breeding grounds. An individual that does not have sufficient resources for moult may not be able to return to the breeding grounds at all. Individuals appear to be also under a time constrain, since early breeding individuals typically fledge more young than later ones in many species (Price and Jamdar 1990). Delayed moult can thus directly result in reduced breeding opportunity.

Our results imply that population size in January can be perfectly predicted from rainfall over the preceding three months. This means that the population is entirely regulated during the winter season, and that breeding and migration have no influence. Limited data on other species shows that their densities (*Phylloscopus magnirostris*) and behaviour (*Acrocephalus dumetorum*) are also affected by dry years, and the influence of climate on population size is likely to be generally strong. Conclusions need to be tempered by the short duration of this study (4 years), and it is possible that in other years breeding and migration success have more influence. In addition, we have not observed the full range of climatic extremes which have been recorded in the winter season (Fig. 11), and the relationship between climate and population size may not be as strong when very dry years are

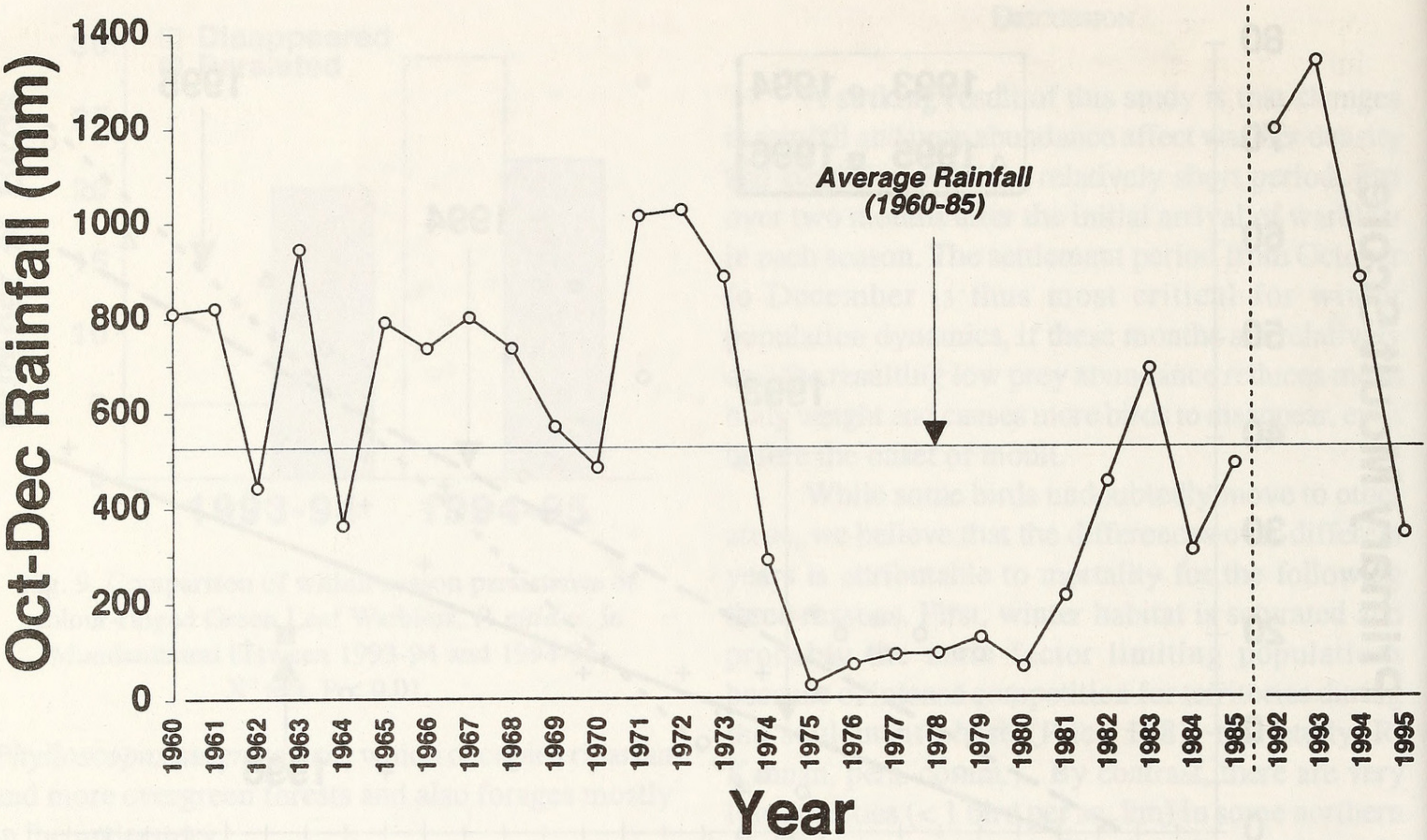

Fig. 11. Winter rainfall (October-December totals) on Mundanthurai plateau during 1960-1985 (data from Tamil Nadu Electricity Board, Lower Papanasam Dam) and 1992-96 (this study, Mundanthurai).

included (although we have no reason to believe that it is not).

Even if there is strong population regulation in the winter, there can be effects of breeding success on local populations. If breeding habitat is unsaturated, then breeding failure in any one locality may result in fewer birds returning to that locality the following year, with possible compensatory increase elsewhere. Several studies in North America (e.g. Holmes *et al.* 1991, Holmes and Sherry 1992) have shown that breeding success does affect recruitment to the populations of the migrant warblers they studied, but possible compensatory effects on populations elsewhere have not been assessed. A second explanation for studies which find an importance of breeding success for migrant species in America and Europe (Böhning-Gaese 1992, Böhning-Gaese *et al.* 1993) is that winter regulation of populations in the Americas and Africa may be less strong than it appears to be in India, because the area of habitat available for over-wintering warblers is probably much less in India. This is especially plausible when viewed in terms of the spatial extent of the breeding areas which are supplying winter migrants. India accommodates many warbler species which breed from the Himalayas north throughout central Siberia and west to Europe.

The Americas and the Europe/Africa migration systems may be different from Asia because of differences in geography, but it is from those systems that most of the data on migrants come (e.g. Fig. 1). The data show both declines and increases of populations at average rates of up to 7% annually, over periods of more than 20 years. Populations have thus changed as much as five-fold over the duration of these studies. We have detected a population decrease of 40% due to climatic change in our four year study, but have not studied very dry years. Thus, it is at least possible that some of the changes in population size of other species are attributable to climate changes, and climate needs to be factored in before more direct human influences on population size are addressed. Our results point to potentially major effects of human-induced climatic changes, such as global warming, on population sizes of different species. They are consistent with the findings of Burton (1995) who has attributed many changes in geographical distribution to recent climate change.

Our study measures the extent to which populations within a single locality are changing, and does not produce an estimate of change in the total numbers of this species. If the inference that habitats are saturated in the winter is correct, then the population size of the species as a whole is likely to be affected by habitat destruction in the wintering range. Few studies have addressed the extent to which population sizes are declining. Perhaps the closest are the breeding bird surveys in North America, which have taken place along the same prescribed routes over many years (e.g. James *et al.* 1996), and show both declines and increases over the past 20-30 years (Fig. 1).

In general, changes in population size depend on the time-scale studied: 10,000 years ago, during the last major ice age, breeding habitat may have been limiting and perhaps the global population was low. We expect the population to have increased since then. The first waves of human-induced habitat change in India occurred a few thousand years ago (Gadgil and Guha 1992), with deforestation accelerating over the past several hundred years (Gadgil 1990, Gadgil and Guha 1992). The subsequent loss of winter habitat may have led to declines over the past few millennia. Habitat destruction has become rampant in recent decades (Rodgers and Panwar 1988, Gadgil 1990, Gadgil and Guha 1992), and its effect on local bird abundance and diversity has been reported (Daniels *et al.* 1990, Price 1990, ICBP 1992).

Extrapolating our four-year study to longer periods based on climate records entails making many assumptions, but can be used to provide a first approximation of the way in which populations have fluctuated in the recent past. We suggest that drought years (especially between 1975 and 1980) must have had dramatic effects on population size. If habitat is further reduced, we may be lulled into a false sense of security by the finding of within-habitat densities, for a single dry year may dramatically alter the picture, and drive populations close to extinction. While this may be a long way off for *P. nitidus*, which is one of the commonest birds in India and a good disperser between patches, the general principles are the same for those less common, poorly dispersing species which are more at risk.

In his later years Sálim Ali became increasingly concerned about habitat conservation. This differed from most other conservation biologists, who then focused mainly on charismatic endangered species, mostly large mammals. In this, as in many other ways, he was ahead of his time, for we now see conservation organizations throughout the world emphasizing environments and not species. In 1979, Sálim Ali discussed the important role insectivorous birds play in the ecosystem, based on studies of the Arthropod pests they consume (Ali 1979). We suspect he was ahead of his time here as well, and suggest that population studies of the commoner elements of India's fauna and flora will play a growing role in habitat conservation. They will provide the litmus test monitoring the state of the environment. We think this is one of many areas of research Sálim Ali would have been actively encouraging, and probably still doing himself, as he entered his second century.

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