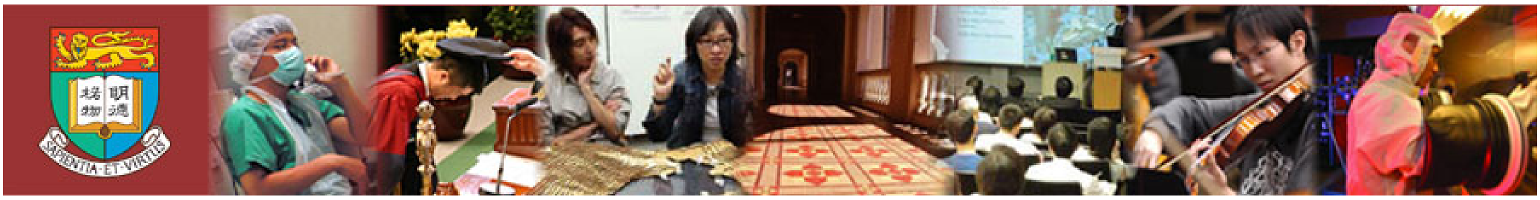

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SHORT COMMUNICATION

Seasonality of forest invertebrates in Hong Kong, South China

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Because of its position on the northern margin of the tropics (22°17′N) and the southern coast of a huge continent, Hong Kong has a climate in which both temperature and rainfall are highly seasonal. Although summer temperatures are equatorial, the January mean is only 15.8 °C, and the absolute minimum recorded at sea level is 0 °C (Dudgeon & Corlett 1994). As a result, all aspects of the ecology of Hong Kong show seasonal changes. The most dramatic changes occur in the bird fauna, with the majority of species migratory (Carey *et al.* 2001). The winter fruiting peak in secondary shrublands and the forest understorey coincides with the arrival of partially frugivorous migrant robins and thrushes (Corlett 1993). However, while resident insectivore-frugivores consume almost entirely fruit during this period (Corlett 1998), all the winter visitors continue to eat insects and some (e.g. *Phylloscopus* warblers) are entirely insectivorous. The study of insect seasonality reported here formed part of a 30-mo study of the seasonality of a forest bird community in Hong Kong (Kwok & Corlett 1999, 2000). Plant names follow Corlett *et al.* (2000).

The main study area was in 30–40-y-old secondary forest, 100–300 m asl in the 460-ha Tai Po Kau Nature Reserve. The forest canopy is dominated by several similar *Machilus* species, 14–18 m tall, while the understorey is dominated by the shrubs *Psychotria asiatica* and *Ardisia quinquegona*. The site is typical of the secondary forest which covers approximately 9% of Hong Kong (Zhuang & Corlett 1997). A secondary study area was established in a 25–

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30-y-old plantation of *Lophostemon confertus*, an evergreen species from subtropical eastern Australia, which is the most widely planted plantation tree in Hong Kong. The canopy height is somewhat lower (10–16 m) than in the secondary forest and the structure more open. The understorey is dominated by the fern *Dicranopteris pedata*, with scattered shrubs of several species.

In the secondary forest, flying insects in the understorey were sampled from February 1993 to June 1995, using four Malaise traps (Kunz 1988), placed approximately 100 m apart. Vegetation immediately around the traps was cut regularly to maintain access to flying insects. Collecting bottles were changed once a week. Although the catch included millipedes and spiders, only insects were analysed. These were classified to order, counted, and the lengths measured to the nearest millimetre. They were then dried at 70 °C to constant weight and each order weighed separately.

Invertebrates on understorey vegetation were sampled by beating shrubs and small trees with a baseball bat over a 1-m × 1-m white plastic sheet. After a pilot study, the procedure was standardized as follows: three plants were chosen haphazardly near each of ten points used for sampling birds, *c.* 80 m apart, and each was beaten three times. Animals falling on the sheet were collected with forceps into 95% alcohol, then sorted, counted, measured, dried and weighed, as above, except that the orders were not weighed separately. This procedure was conducted monthly from February 1993 to February 1994, in odd number months from March 1994 to February 1995, and then monthly again until June 1995.

Litter invertebrates were sampled by removing, by hand, all leaf litter and loose surface soil in 25-cm × 25-cm perspex quadrats. After a pilot study, 30 samples were taken each time, three placed haphazardly near each of the 10 bird sampling points. Invertebrates were separated out visually in the field on a white tray and transferred to 95% alcohol, before sorting, counting, measuring, drying and weighing as above. This procedure was conducted monthly from January 1993 to February 1994 and then in even number months until February 1995.

In the *Lophostemon* plantation, invertebrates were sampled by the same three methods between March 1994 and February 1995. Only two Malaise traps were used but sampling effort was the same as in the secondary forest for invertebrates on understorey vegetation and in litter, except that the 30 samples were spread over only four bird sampling points. The results from the plantation were, in general, very similar to those from the secondary forest, so they are not reported in detail here.

All-subsets regression was used to investigate the relationship between the number (and log-transformed number) and biomass of invertebrates and the weather variables suggested by the invertebrate-seasonality literature. These included aspects of the temperature, relative humidity and rainfall for the sampling day and for the week, two weeks and month preceding the sampling day, plus the rainfall for the periods 8–14 and 15–28 d preceding the sampling day. The 'best' regression models were selected on the basis of the adjusted R-square (adj-R^2) and Mallow's C_p. Models which did not explain a biologically meaningful proportion of the variation (adj-R^2 < 10%) were rejected. Note that individual weeks and months are not mutually independent because they form a time series.

The bird community of the main study area was sampled over the same time period, using the point count method to estimate bird densities (Kwok & Corlett 1999). Sampling intervals were different for birds and invertebrates, so mean bird densities in the weeks when the invertebrates were sampled were used in regression analyses. The birds were divided into feeding guilds (insectivores, insectivore–frugivores and both together) and the total density and biomass of each guild were used as independent variables in simple linear regressions on total number and total biomass of aerial insects and, separately, invertebrates on understorey vegetation. The density and biomass of ground-feeding birds were regressed on the number and biomass of litter invertebrates.

In the secondary forest, the 53 897 insects caught in the Malaise traps were dominated numerically by Diptera (80.6%), followed by Coleoptera (6.3%), Lepidoptera (5.3%) and Hymenoptera (3.9%). Hymenoptera (25.5%) and Lepidoptera (18.3%) dominated the biomass. There was no regular seasonal pattern in the total number of insects because of dominance by the Diptera, which varied aseasonally (Figure 1). The number of Coleoptera also showed no clear seasonal pattern, although the lowest numbers were in winter. In contrast, numbers of both Hymenoptera and Lepidoptera varied seasonally, with winter lows and early summer maxima. Biomass was highly seasonal, with a winter low, for total insects and each order separately, except the Diptera. Both the composition at the order level and the temporal trends were very similar at the plantation site, but the numbers and biomass per trap were usually higher, except for the Coleoptera.

The 3394 invertebrates caught by beating were dominated numerically by Collembola (21.4%), Psocoptera (21.0%), spiders (16.7%) and ants (14.9%). The total number of invertebrates varied seasonally, with an August–October low and an April–May maximum (Figure 1). The pattern with biomass was similar, except for a peak in September 1993 caused by a single, large grasshopper. As with the Malaise traps, the results from beating at the plantation site were very similar to those from the secondary forest, but, in this case, numbers were always lower and biomass usually so. The 903 invertebrates caught in the litter quadrats were dominated numerically by the Isopoda (38.0%), ants (16.8%), termites (13.2%) and spiders (11.0%). The total number and biomass of litter invertebrates showed similar seasonal trends, with winter minima (Figure 1). Again, the results from the plantation site were very similar but both numbers and biomass were always lower.

Most invertebrates caught by all three sampling methods were < 4 mm long

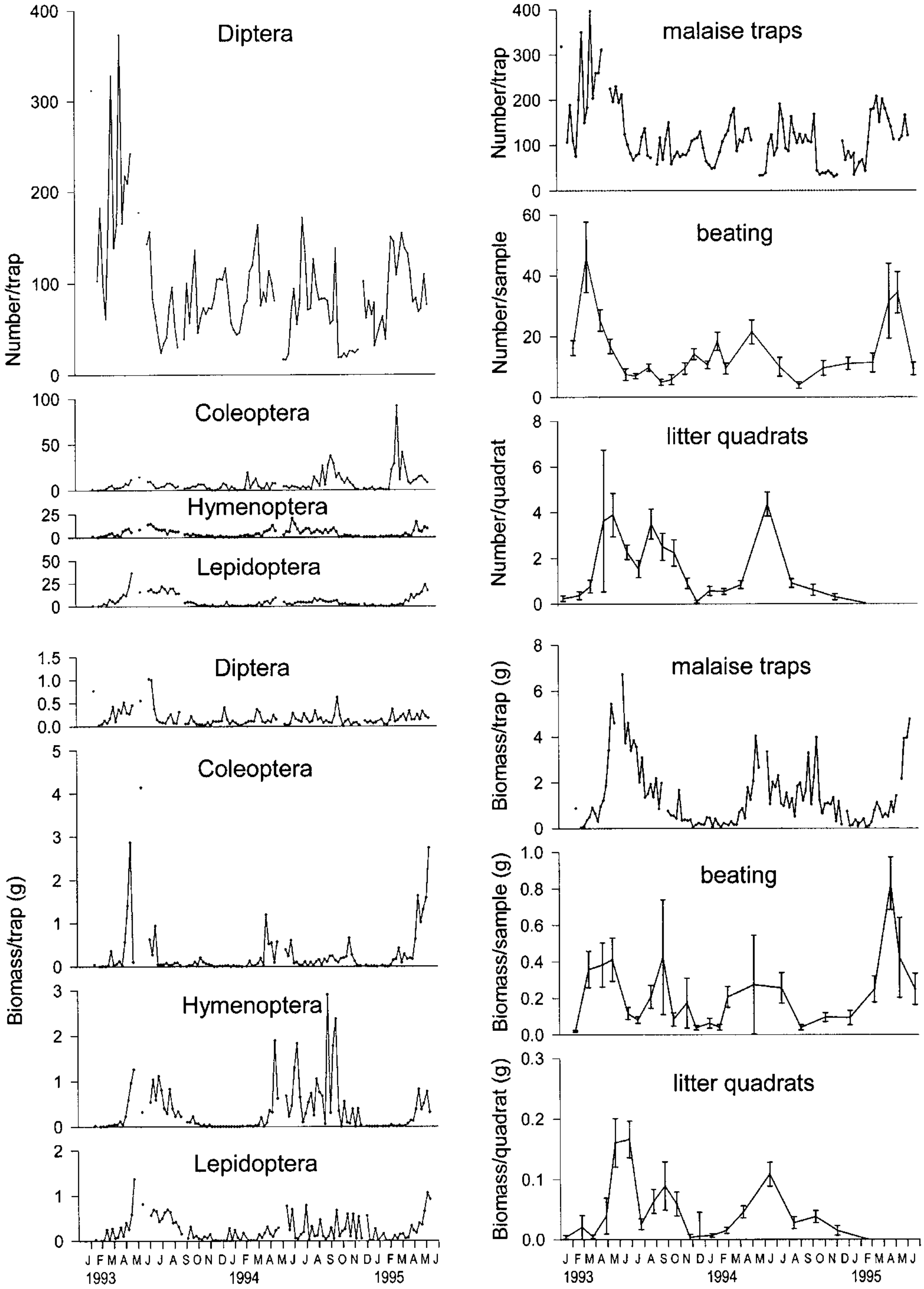

Figure 1. Invertebrate abundance in Hong Kong secondary forest between February 1993 and June 1995. Left: numbers and biomass of Diptera, Coleoptera, Hymenoptera and Lepidoptera caught per Malaise trap. Right: total numbers and biomass of invertebrates caught in Malaise traps, by beating understorey vegetation, and in litter quadrats. Error bars are standard errors.

Table 1. Size class distributions of invertebrates in Malaise traps, on understorey vegetation, and in litter quadrats, from May–August (breeding season), when resident birds are feeding their juveniles, and from November–February (winter), when migrants are abundant and no birds are breeding. The figures are mean numbers in each size class per survey.

Size class (mm)	Malaise traps		Beating		Litter	
	Breeding	Winter	Breeding	Winter	Breeding	Winter
0–2	277.8	202.3	39.4	81.7	8.3	3.8
2–4	113.7	52.2	71.0	36.7	29.8	5.3
4–6	33.7	6.7	8.3	6.6	7.8	4.8
6–8	29.3	4.0	10.4	1.9	4.0	2.5
8–10	29.7	3.3	4.5	1.0	2.8	1.3
10–12	8.8	2.2	5.9	0.3	3.2	0.4
12–14	2.4	0.4	4.6	0.1	1.0	0.4
14–16	7.3	1.4	11.4	2.0	2.3	0.6

(Table 1). The size class distributions varied seasonally, with a higher proportion of larger invertebrates in May–August, when resident bird species are feeding their juveniles, than in winter (November–February).

No regression model explained a biological meaningful percentage (> 10%) of the variation in total number of aerial insects or Diptera, or the biomass of Coleoptera or Diptera. The best models for the total aerial insect biomass and the numbers and biomasses of other orders included only the mean of daily mean, maximum or minimum temperatures during the week the traps were open (Table 2). These three temperature variables are very highly correlated with each other ($r > 0.98$). For invertebrates caught by beating, the only models which explained more than 10% of the variation were one for ant numbers, which included both the mean temperature of the preceding week and the mean relative humidity on the sampling day, and one for total invertebrate biomass, which included only the mean relative humidity of the preceding

Table 2. Regression models relating invertebrate number or biomass in a Hong Kong secondary forest to weather factors. Only models with adj-R^2 > 10% are shown. $P > 0.001$ for all models shown.

Dependent variable	Predictor(s)	adj-R^2
Malaise traps		
Total insect biomass	week–min T	45.1
Log (Coleoptera numbers)	week–max T	23.3
Log (Hymenoptera numbers)	week–mean T	69.1
Hymenoptera biomass	week–mean T	69.1
Log (Lepidoptera numbers)	week–mean T	71.1
Lepidoptera biomass	week–min T	71.1
Beating of understorey vegetation		
Total invertebrate biomass	week–mean RH	20.1
Hymenoptera (ant) numbers	week–mean T, day–mean RH	46.5
Litter quadrats		
Total invertebrate numbers	month R	48.3
Hymenoptera (ant) numbers	week R, month R	64.0
Spider numbers	week R, month R	77.8
Isopoda numbers	month-mean T, week R	38.0

T = temperature, RH = relative humidity, R = rainfall; day = the sampling day, week = the week preceding the sampling day, month = the month preceding the sampling day.

week. The best model for total litter invertebrate number included only the total rainfall of the preceding month. For individual orders, the best models for the numbers of ants, spiders and isopods all included some aspect of rainfall, along with the mean temperature of the preceding month for the isopods. Total bird density was at a maximum in the secondary forest from December to June, and insectivore density was at a maximum in January and February (Kwok & Corlett 1999). The only relationships with invertebrate abundance which 'explained' more than 10% of the variation in bird abundance were negative.

An earlier study in Hong Kong used two Malaise traps and seven impaction traps (which caught mainly Coleoptera) in a narrow strip of secondary forest along a stream, in order to assess insect availability to bats (Ades & Dudgeon 1999). As in the present study, the Malaise catches were dominated numerically by Diptera, followed by Hymenoptera, Lepidoptera and Coleoptera. In contrast to the present study, however, total numbers of flying insects were strongly seasonal, with a dry-season low, a steep rise in March, and then a decline from June onwards. These differences may reflect the buffering effect on understorey microclimate and thus insect numbers provided by the much larger forest area at Tai Po Kau, but further studies would be needed to confirm this. As at Tai Po Kau, the Diptera showed less seasonality than other invertebrate groups, which is consistent with their importance as visitors to, and probable pollinators of, winter-flowering shrubs and trees in Hong Kong (Corlett 2001).

Similar invertebrate seasonality was found in the upland tropical rain forest of northern Queensland (19°S), Australia, which has a similar climate, except for the smaller annual temperature range (Frith & Frith 1990). At this site, both the number and biomass of insects caught in Malaise traps was lowest in the early dry season. Numbers of litter invertebrates (mainly amphipods and insect larvae, followed by ants and Isopoda) increased at the end of the cool, dry season and peaked during the warm, wet season. A similar seasonal pattern of arthropod abundance was also found by a nocturnal visual census in the understorey of the Atlantic coastal forest of south-east Brazil (24°S), again with similar rainfall seasonality to Hong Kong but less variation in temperature (Develey & Peres 2000). Ants were excluded and the counts were dominated by spiders, Orthoptera and Blattodea.

Both the above studies concluded that rainfall seasonality was a more important influence on invertebrate numbers than temperature seasonality, as seems to be generally true for tropical sites (Wolda 1988). Temperature is more important in the subtropics (e.g. Basset 1991) and the temperate zone. Hong Kong has a high degree of temperature seasonality for the tropics and temperature was the best predictor for aerial insect abundance. However, relative humidity and rainfall appeared, respectively, in models for insects caught by beating and for litter invertebrates. Many studies have also provided evidence of a link with plant phenology, with invertebrate abundance peaking during the period of maximum young leaf availability. This is consistent with the pattern for invertebrates on understorey vegetation, with a minimum in late summer, but separating the influences of temperature, rainfall and plant phenology is difficult because all three show a basically similar seasonal pattern in Hong Kong. Many of the regression models explained relatively little of the variation in invertebrate abundance, which should not be surprising, given the large number of species involved and the many direct and indirect ways in which weather could separately influence the abundance of each species.

The abundance of birds did not match the availability of their invertebrate prey. The maxima in both total bird density and insectivore density at the site overlap with the December–March low in invertebrate abundance. Small insects are still available in winter and most of the winter-visitor insectivores are small *Phylloscopus* warblers, that presumably feed on such insects. Greenberg (1995) suggested that the availability of large insects for feeding juveniles during the breeding season may limit the resident bird populations to a density that leaves surplus food in winter. As with other tropical studies (Basset & Kitching 1991), most invertebrates sampled in this study were small, and the increase in the proportion and number of large insects in April–May coincides with the start of the breeding season for resident birds. This is consistent with Greenberg's hypothesis, but we lack evidence that the availability of large insects limits breeding success and that the resultant resident bird densities are too low to exclude migrants.

The lower number and biomass of invertebrates on understorey vegetation and in litter in the *Lophostemon confertus* plantation probably reflect its greater openness and thus drier environment. The abundance of litter invertebrates may also have been affected by the predominance of the tough, decay-resistant leaves of *Lophostemon*. The higher catches of aerial insects in the plantation are surprising, but could also reflect its relative openness, which may increase the catchment area for each trap. The plantation site had less than a third of the mean total bird density of the secondary forest (Kwok & Corlett 2000), which may be, in part, a consequence of these differences in invertebrate availability.

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