

TABLE 1. Time devoted by polar bears to certain categories of behaviour during the summers of 1969 and 1970

| Classification of bear | No. of observation periods | Feeding | | Resting | | Travelling | | Total | | | | | |
|------------------------|----------------------------|---------|-----|---------|----|------------|------|-------|-----|------|-----|----|-------|
| | | h | min | % | h | min | % | h | min | % | | | |
| Lone bears | 29 | 1 | 51 | 2.4 | 67 | 10 | 86.4 | 8 | 44 | 11.2 | 77 | 45 | 100.0 |
| Females with cubs | 10 | 1 | 40 | 4.9 | 29 | 39 | 87.7 | 2 | 29 | 7.4 | 33 | 48 | 100.0 |
| All bears | 39 | 3 | 31 | 3.2 | 96 | 49 | 86.8 | 11 | 13 | 10.0 | 111 | 33 | 100.0 |

travelling, $\chi^2 = 0.63$, $p = 0.73$; feeding, $\chi^2 = 1.13$, $p = 0.59$).

feeding, and the variability in abundance and dispersion of food items between years.

Discussion

These data suggest that the bears were living mostly on stored fat, and conserving energy at the same time by resting extensively. This conclusion is supported by the fact the bears appeared to be fat when they arrived on the island. However, these data form a time budget, not an energy budget, and therefore provide only an indirect measure of food intake. Moreover, they represent only daylight hours, and are heavily biased toward the centre of the day. A final decision about the option chosen by polar bears, or rather the degree to which each option is utilized, should be reserved until information can be gathered on the activities of polar bears at night, the actual amount of food acquired during

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- JONKEL, C. J., P. SMITH, I. STIRLING, and G. B. KOLENOSKY. 1976. The present status of the polar bear in James Bay and Belcher Islands area. *Can. Wildl. Serv. Occas. Pap.* 26.
- KNUDSEN, B. 1973. The ecology of polar bears on North Twin Island, Northwest Territories. M.A. Thesis, University of Montana, Missoula, Montana.
- RUSSELL, R. H. 1975. The food habits of polar bears of James Bay and southwest Hudson Bay in summer and autumn. *Arctic*, 28: 117-129.
- SIEGEL, S. 1956. *Non-parametric statistics*. McGraw-Hill, New York.

Head flicking by tent caterpillars: a defensive response to parasite sounds

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Western tent caterpillars respond to sounds of 300-2100 Hz by head flicking. The sound frequencies to which they are most sensitive match the flight sound of a fly parasite which lays eggs on the heads of caterpillars. Caterpillars on tents are more likely to head flick when stimulated by sound and have lower parasitization levels than fifth-instar caterpillars which have left the tent.

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Les chenilles de la livrée de l'ouest réagissent à des sons de 300 à 2100 Hz par des hochements de tête. La fréquence des sons auxquels les chenilles sont le plus sensibles correspond à celle du bruit de vol d'une mouche parasite qui pond ses œufs sur la tête des chenilles. Les chenilles qui vivent encore sur les nids ont une réaction plus vive à l'audition du son; elles ont aussi un taux de parasitisme moins élevé que les larves de cinquième stade qui ont déjà quitté les nids.

[Traduit par le journal]

Responses to sound by caterpillars were first recorded by Bonnet (1779,¹ cited in Minnich 1935). Since then the sound response of caterpillars of a number of species of Lepidoptera has been tested (Minnich 1935). Three responses occur among the species tested: stopping, freezing with the head thrown back, and head flicking. These behaviours appear defensive, but we know of no studies on their functional importance.

Particularly on warm spring days, tent caterpillars, *Malacosoma pluviale* (Dyar), can be seen with almost every individual in a colony head flicking violently. Sounds such as human coughs or flying bumble bees appear to elicit this behaviour. We observed wasp parasites being knocked from the tent by a head-flicking caterpillar and predicted that this behaviour would deter oviposition by other parasites as well. Four parasites have been recorded attacking tent caterpillars in British Columbia: a braconid wasp, an ichneumonid wasp, and two tachinid flies (Iwao and Wellington 1970). One of the tachinids, *Tachinomyia similis*, lays eggs directly on the head capsule of the caterpillar (Fig. 1). The egg must be laid on the caterpillar head or the caterpillar can remove it with its mouth parts. We hypothesized that sound reception in caterpillars might allow early detection of approaching parasites and head flicking could then prevent their successful oviposition.

We are reporting this study as a note because tent caterpillar populations in British Columbia have crashed and sufficient numbers will not be available for further studies for several years. We hope that others might consider the interaction between sound and head flicking in other caterpillars and sawfly larvae.

Materials and Methods

Study Population

The population of tent caterpillars which we studied lives on Mandarte Island, in the Haro Strait, 8 km east of Sidney, British Columbia, Canada. Wild rose (*Rosa nutkana*) is a major component of the shrub vegetation there and is the primary food plant of the tent caterpillars. Caterpillars emerge from eggs in middle to late April and by late May have reached the fourth instar. Western tent caterpillars spend a large portion of their time sitting on the outer surface of their silk tents until the fifth instar, when they spread out from the original colony and become solitary, before pupating at the end of this instar.

Sound Recordings

Pure-frequency synthetic sounds were obtained from a frequency generator and recorded on a Uher tape recorder (model 4000L report). The sound of flight of the flies was recorded at room temperature on the same tape recorder and analyzed with a Kay missilyzer spectrograph (Kay Electric Company, Pine Brook, NJ).

Field Tests

The response of caterpillars to sound frequencies was measured as the proportion of caterpillars which reacted to the sound by head flicking. For each frequency 200–350 individuals on at least 10 tents were tested. Groups were often retested at a different frequency after the group had become quiet. Tests were done at 20–25°C. Parasitized and nonparasitized solitary fifth-instar caterpillars were tested in the field on vegetation or on the ground. Other solitary fifth instars were collected and their response to sound tested on a flat surface out of doors. Fourth-instar caterpillars were collected from tents and tested in a similar manner. The same caterpillars were tested at all frequencies with the exception of the flat-surface tests of the solitary fifth instars in which one group of 52 caterpillars was tested at all five frequencies and an additional group of 85 tested at three of the frequencies. Because there were so few fifth-instar caterpillars on tents, these were not used to test the response of caterpillars removed from tents.

Sounds were played within approximately 20 cm of the tent. The intensity of sound was measured in the laboratory with a Realistic music sound level meter at 20 cm from the tape recorder speaker. We do not know how this sound intensity relates to that of an approaching fly which may come in actual contact with the caterpillar. Because there is a gull colony on Mandarte, the background noise level is often high. A study of courtship sounds of *Drosophila* (von Schilcher 1976) used playbacks at 105 dB, which is similar to the sound intensities we used. There was no obvious association between sound pressure and caterpillar response (Table 1).

Results

A tape recording of a flying *Tachinomyia* caused head flicking by the caterpillars and the sound of the tachinid flight clearly falls in the range of responsiveness of the caterpillars (Fig. 2, Table 1). Therefore, the caterpillars can perceive the sound of approaching parasitic flies.

We next wanted to know how effective head flicking was as a defensive reaction. If caterpillars vary in their response to sound, as indicated by the fact that all caterpillars on a tent did not always head flick, parasitized caterpillars might be expected to be less responsive to sound than would nonparasitized caterpillars. Tests of solitary fifth-instar caterpillars showed no difference between parasitized and nonparasitized caterpillars, but all solitary caterpillars were much less responsive than those on tents (Table 1).

This observation suggested that comparison of parasitization rates of solitary caterpillars (non-responsive) with those on tents (responsive) might indicate the effectiveness of head flicking. Caterpillars off the tents had significantly higher rates of parasitization (Table 2).

Two explanations for the reduced responsiveness of solitary caterpillars are that (1) caterpillars undergo a physiological change on leaving the tent which lowers their responsiveness to sound or (2) some component of the tent environment aids responsiveness. To distinguish these possibilities, solitary fifth-instar caterpillars and fourth-instar

¹Oeuvres d'histoire naturelle et de philosophie. Tome 2.

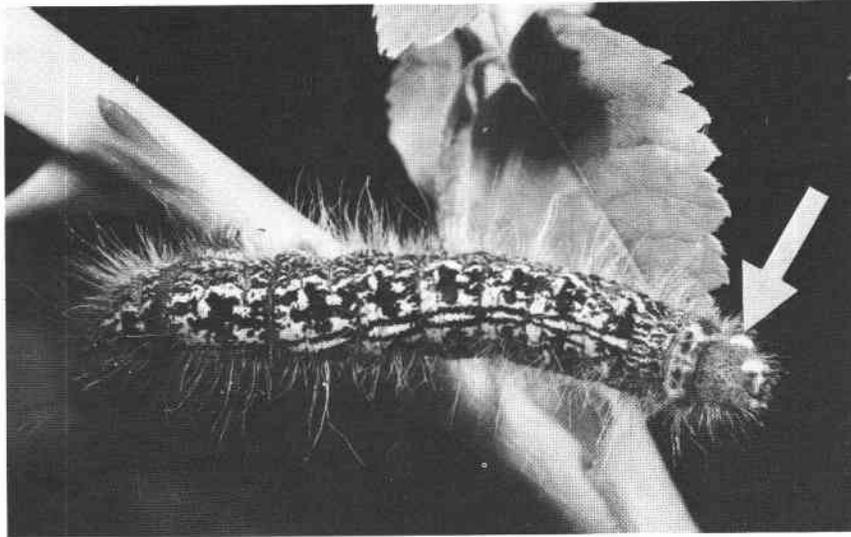


FIG. 1. Fifth-instar western tent caterpillar with eggs of the parasitic fly *Tachinomyia similis* on the head capsule (arrow).

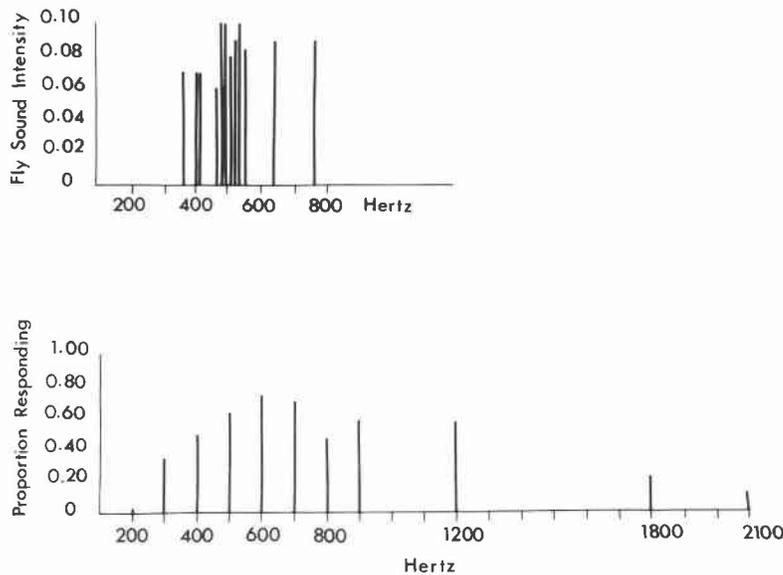


FIG. 2. Response of fourth- and fifth-instar tent caterpillars to sound frequencies measured as the proportion of caterpillars which reacted to the sound by head flicking. An amplitude frequency section of the flight sound is given on the upper part of the figure represented on a proportional scale.

caterpillars from tents were collected and tested individually on a flat surface.

Caterpillars tested on a flat surface frequently responded by stopping when the sound was turned on, but they rarely performed head-flicking behaviour (Table 1). The proportion of caterpillars responding to different sound frequencies by stopping was similar to that which head flicked while on the tents in response to the same frequencies.

From this experiment we conclude that caterpillars

removed from the tent environment can still hear the sounds, but are far less likely to perform head flicking. Future work might consider if the tent is the necessary component for a high frequency of head flicking, or if the presence of other caterpillars is responsible for the increased head flicking by caterpillars here. For this study, the interesting observation is that the groups of caterpillars which do not head flick have higher rates of parasitization.

TABLE 1. Proportion of tent caterpillars responding to sound by head flicking or stopping (flat-surface tests only). Number tested for each frequency is in parentheses. Head flicking is significantly reduced in solitary caterpillars (χ^2 test, $P < 0.01$) but the response to sound measured by stopping crawling is not significantly changed

| Frequency, Hz | Sound pressure, dB | On tents | Flat surface | | | | | | |
|---------------|--------------------|-----------|--------------|----------|-----------|----------|-----------|-----------|--|
| | | | Solitary | | From tent | | Solitary | | |
| | | | Eggs | No eggs | Flick | Stop | Flick | Stop | |
| 400 | 95 | 0.49(330) | | | | | | | |
| 450 | 92 | | | | 0.03(40) | 0.35(40) | 0.04(137) | 0.38(137) | |
| 600 | 95 | 0.73(348) | 0.16(25) | 0.18(22) | | | 0.12(52) | 0.81(52) | |
| 900 | 104 | 0.57(343) | 0.18(17) | 0.08(26) | 0.06(40) | 0.55(40) | 0.12(137) | 0.61(137) | |
| 1200 | 98 | 0.57(260) | | | | | 0.12(52) | 0.71(52) | |
| 1800 | 105 | 0.23(309) | | | 0.03(40) | 0.40(40) | 0.01(137) | 0.33(137) | |

TABLE 2. Parasitization rates of caterpillars on and off tents

| Type of caterpillar | % parasitized | No. |
|------------------------|---------------|-----|
| Fifth instar, solitary | 52* | 121 |
| Fifth instar, tent | 12 | 49 |
| Fourth instar, tent | 4 | 137 |

*Parasitization rate significantly greater (χ^2 test, $P < 0.01$) than tent caterpillars on tents. Fourth- and fifth-instar caterpillar parasitization rates are not significantly different.

Discussion

Colonial caterpillars such as tent caterpillars are conspicuous and, one would think, easily located by parasites. But *Tachinomyia similis* seems to prefer to parasitize caterpillars after they have left the tent. We have suggested that this might be associated with reduced defensive reaction of solitary caterpillars. It could also be that the parasites prefer the largest caterpillars as hosts. These two characteristics can not be easily separated experimentally and in fact may combine to determine host preference.

If caterpillars are better protected on the tents, why do the fifth instars leave the tents? Perhaps fifth-instar caterpillars require more food than is available in the immediate vicinity of the tent and must go further afield to find food.

Some *Tachinomyia* flies successfully parasitized caterpillars on tents. This may simply be because head flicking sometimes fails as a defense, or because eggs were laid while the caterpillar was off the tent feeding. However, another aspect of fly behaviour gives them an advantage. The threshold temperature for flight of the *Tachinomyia* was 15°C but head flicking of caterpillars was reduced below 17°C. Therefore, flies are still active when caterpillars are less responsive to their flight sounds.

Though many caterpillars respond to sounds in the 200–500 Hz range (Minnich 1935), others do not. Cinnabar moth larvae (*Tyria jacobaeae*) which head flick in response to touch and loud sounds (Myers and Campbell 1976) showed no response to the frequencies which stimulated tent caterpillars. Therefore, although sound responsiveness is a general characteristic of caterpillars, the details of the response vary from species to species. It is likely that this variation is a result of different selection pressures related to the types of predators and parasites which normally attack the species.

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IWAO, S., and W. G. WELLINGTON. 1970. The western tent caterpillar: qualitative differences and the action of natural enemies. *Res. Popul. Ecol.* **12**: 81–99.

MINNICH, D. E. 1935. The responses of caterpillars to sounds. *J. Exp. Zool.* **72**: 439–453.

MYERS, J. H., and B. J. CAMPBELL. 1976. Indirect measures of larval dispersal in the cinnabar moth, *Tyria jacobaeae* (Lepidoptera: Arctiidae). *Can. Entomol.* **108**: 967–972.

VON SCHILCHER, F. 1976. The function of pulse song and sine song in the courtship of *Drosophila melanogaster*. *Anim. Behav.* **24**: 622–625.