Behaviors of Western Spruce Budworm Moths (*Choristoneura occidentalis*) as Defences Against Bat Predation

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We investigated potential defense behaviors of adult western spruce budworm (Choristoneura occidentalis), *a non-auditive lepidopteran, against bat predation. Although western spruce budworm moths started to fly before sunset, earlier than many species of moths, temporal isolation of flying moths from foraging bats was incomplete as moths were most active after sunset once bats were foraging. Flying* C. occidentalis *were most active close to their host trees, and thus were isolated from some bat activity because vegetation limits foraging by some bats. Moths mostly flew near the tops of trees, an area that may have a high predation pressure from bats. Resting western spruce budworm spent little time fluttering their wings or crawling, behaviors that are used as cues by gleaning bats. The outbreak nature of this species, in which large numbers of moths are active at one time, may allow dilution effects to reduce predation risk.*

KEY WORDS: lepidoptera; bats; chiroptera; British Columbia; behavior; predation.

INTRODUCTION

Lepidopterans are a main prey of many species of insectivorous bats (e.g. Jones and Rydell, 2003). In response, audition has evolved in a number of families of moths (Hoy and Robert, 1996), enabling them to hear the echolocation calls of approaching bats. Upon the detection of a bat, these moths use evasive flight maneuvers to escape predation (Lewis *et al.*, 1993).

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In contrast to the defenses of auditive species, defenses used by earless moths against bat predation have not been studied in detail (Morrill and Fullard, 1992). Earless moths may use temporal, spatial, and behavioral isolation, as well as flight behaviors, in defense against bat attacks (Fullard, 1998; Rydell, 2004). Modification of moth behavior, such as advancing or delaying peak activity to periods when bats are not foraging, or being most active in areas which are difficult for bats to forage in, such as dense foliage, could decrease predation risk. Spatial isolation would be most adaptive against aerial-hawking bats, but even maneuverable, gleaning species of bats cannot penetrate dense foliage (Jensen *et al.*, 2001). Being active near foliage may also help reduce bat predation because in such a situation a bat must be able to detect moths within a cluttered environment where echoes from vegetation could obscure echoes from moths (Jensen *et al.*, 2001). Some species of earless moths tend to fly close to the ground, providing protection because the moths are not active at heights bats usually forage at (Fullard and Napoleone, 2001).

The western spruce budworm (*Choristoneura occidentalis*; Tortricidae), as well as its eastern counterpart, *C. fumiferana,* has been studied extensively (Sanders, 1991). The western spruce budworm occurs from the Fraser River in British Columbia to southern Arizona and New Mexico. Host plants are predominantly Douglas-fir (*Pseudotsuga menziesii*), true firs, spruce, hemlock and larch trees (Sanders, 1991). *C. occidentalis* is an outbreak species in which adult moths emerge from pupation in large numbers. Adult moths live for 10 to 14 days in late July to early August (Sanders, 1991). There is only one generation a year. Larvae feed on the buds and developing cones of the host trees, damaging the needles and causing them to turn reddish, which is visible during and after an outbreak of moths. The defoliation can cause reduced growth, top-kill, reduced lumber quality and sometimes tree mortality (Alfaro, 1986). For this reason, budworm species are considered forest pests, and defoliation has driven the extensive research on them (Sanders, 1991).

Bats could be involved in reducing levels of spruce budworm during outbreaks. Tortricid moths such as *C. occidentalis* are not known to detect the echolocation calls of bats (Fullard and Napoleone, 2001). Thus, our goal was to determine whether western spruce budworm have other defense mechanisms to decrease their vulnerability to bats.

METHODS AND MATERIALS

We observed the activity of bats and *C. occidentalis* at 12 field sites near the city of Merritt, in the southern interior of British Columbia,

between 13 July and 6 August, 2003. Western spruce budworm was at the peak of its population cycle during our study (L. Maclaughlan, pers. comm.). All study sites were situated in Douglas-fir forests.

The bat fauna of our study area includes *Eptesicus fuscus, Myotis lucifugus, M. volans, M. yumanensis, M. evotis* and *M. californicus*. These bats have a variety of foraging techniques (Fenton and Bell, 1979), including aerial-hawking (hunting for flying insects), and gleaning (capturing insects from substrate surfaces). These two foraging tactics involve differences in echolocation and degrees of maneuverability (Faure and Barclay, 1994). *E. fuscus* is one of the largest species in our study area and captures prey by aerial hawking (Kurta and Baker, 1990). Most *Myotis* species also hunt flying prey, while *M. evotis* forages by gleaning and aerial hawking (Faure and Barclay, 1994). All species include moths as a major part of their diet in our study area (Wilson, 2004).

We measured bat activity at the field sites by recording the echolocation calls of flying bats for 3.5 h after sunset using a remote-system Anabat II ultrasound detector (Titley Electronics, Ballina, Australia). There was a minimum of 100 m between the bat detector and the moth observation area, to minimize interference between them. The detector was set 1 m off the ground at the edge of a forest clearing, pointing up at a 45° angle, with sensitivity at 8. We counted the number of bat passes, defining a 'pass' as ≥ 2 calls, separated from other calls by ≥ 1 s (Thomas, 1988). In most cases, moth observations and bat activity sampling took place on the same night, but in some cases they were done on different nights but at the same field site. We also measured ambient temperature at the field site with a Thermocron temperature sensor (ibutton; Dallas Semiconductor, Dallas, TX).

To observe budworm moth behavior, we selected trees around which *C. occidentalis* moths were flying, and set up a tripod approximately 5 m from the base of a tree. A tube (3.9 cm diameter) was attached to the tripod and oriented so that the top of the tree could be viewed though it. The tree-top took up approximately one quarter of the field of view through the tube. We observed the tree through the tube, keeping the same part of the tree and the sky in view, and counted moths for one minute every 20 min. Every moth that flew into the field of view was counted. Although some moths may have flown into view more than once, we wanted a measure of moth activity, rather than the absolute number of moths. Although we could not specifically identify each moth we observed, *C. occidentalis* dominated light-trap captures in our study area (Wilson, 2004), and the flight timing and behavior of the moths we observed were typical of western spruce budworm. We used a spotlight during the one-minute intervals after sunset to illuminate the area being observed. The spotlight was only on during the minute

while observing. We did not detect any increase in moths flying into the light during the interval, nor did it appear to alter the moths' behavior or increase the number of moths seen. A night vision scope proved ineffective in allowing us to observe flying moths.

Four times during the night, starting one hour before sunset, we recorded the spatial distribution of flying moths using the above method. In addition to the counts of moths flying near the tree (0 m from the tree), we positioned the tripod 1, 3, and 5 m away from the 0 m position, maintained the same orientation of the tube, and counted moths for one minute at each position. We thus counted moths at 0, 1, 3 and 5 m from the tree.

We collected data regarding the height of moths flying around trees from approximately 10 m from the base of a selected tree. We selected trees so that we could backlight the branches against the sky, and increase counting accuracy by avoiding overlap with other trees. We collected height data before and after sunset on two trees at each site. These counts were made by viewing through a 5 cm-diameter tube for one-minute intervals at each of five relative heights (bottom, bottom-middle, middle, middle-top and top). As we used a spotlight to illuminate the sections of the tree during observations after sunset, the heights were observed in random order to minimize effects of the light source.

We observed the behavior of individual moths throughout the night, both before and after sunset. We verbally recorded the sequence of behaviors such as flying, stationary (moth not moving on a tree branch), wing fluttering (while moth was on a tree branch), or crawling (on a tree branch), onto a tape recorder while watching a single individual. To determine the sex ratio of flying moths, we used a sweep net before and after sunset, to capture flying moths up to 3 m from the ground and up to 5 m from trees. We determined the sex of each individual.

We calculated relative bat activity for each 10-min interval by dividing the number of bat passes from each interval by the total number for that night. We did the same for moth activity for each observation period. We used analysis of covariance to analyze the distance and height data, and the behavior of individual moths (SAS Version 8.1). Moth numbers were log or square-root transformed to meet the assumptions of normality for the distance and height data, respectively. We report all values as mean $\pm$ standard error (SE). Because transformed data were back-transformed for presentation, error bars are asymmetrical. Individual observational data of crawling and fluttering behaviors were analyzed using χ^2, two-by-two contingency tests with Yate's continuity correction (Zar, 1984). Sex ratio data were analyzed using χ^2 tests with Yate's continuity correction. All tests employed a rejection criterion of 0.05.

RESULTS

Moth activity varied through the late afternoon and night. Activity was low in the late afternoon, but increased in the early evening before sunset, and peaked an hour after sunset (Fig. 1). This peak was just after the first peak in bat activity. Moth activity gradually declined until 220 min after sunset, when our observations stopped. Bats became active starting 30 minutes after sunset and had three peaks in activity, one 40 min after sunset, another 90 min after sunset, and one 190 min after sunset. There was little bat activity from 100 to 150 min after sunset (Fig. 1).

Flying moths were most active close to trees. After removing non-significant interactions, the ANCOVA model analyzing variation in the distance of moths from trees contained time (relative to sunset) and distance from the tree as main effects, and ambient temperature as a covariate. The model explained a significant amount of variation in number of moths observed ($F = 16.72$, $df = 7, 208$, $p < 0.001$). The number of moths varied with distance from the tree ($F = 29.73$, $df = 3, 208$, $p < 0.001$; Fig. 2). In particular, there were more moths at the closest distance from the tree than at
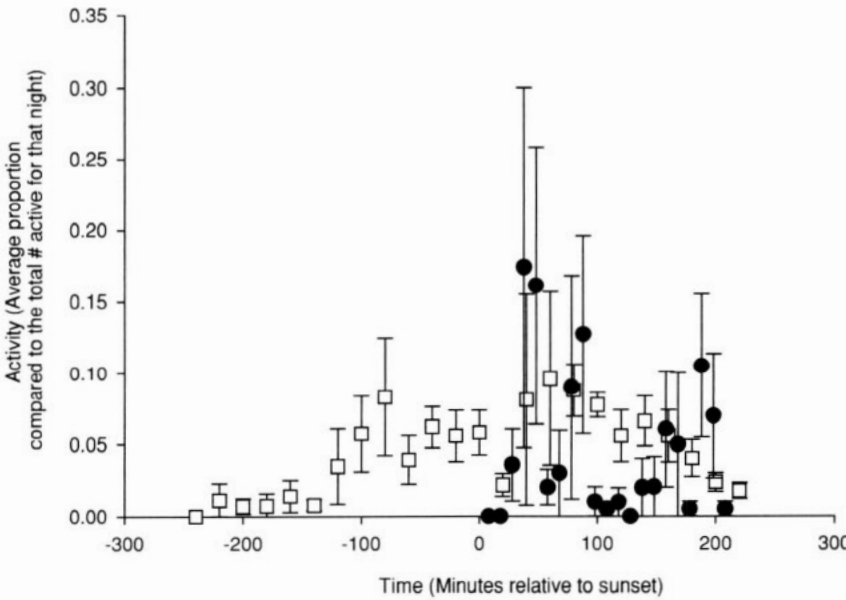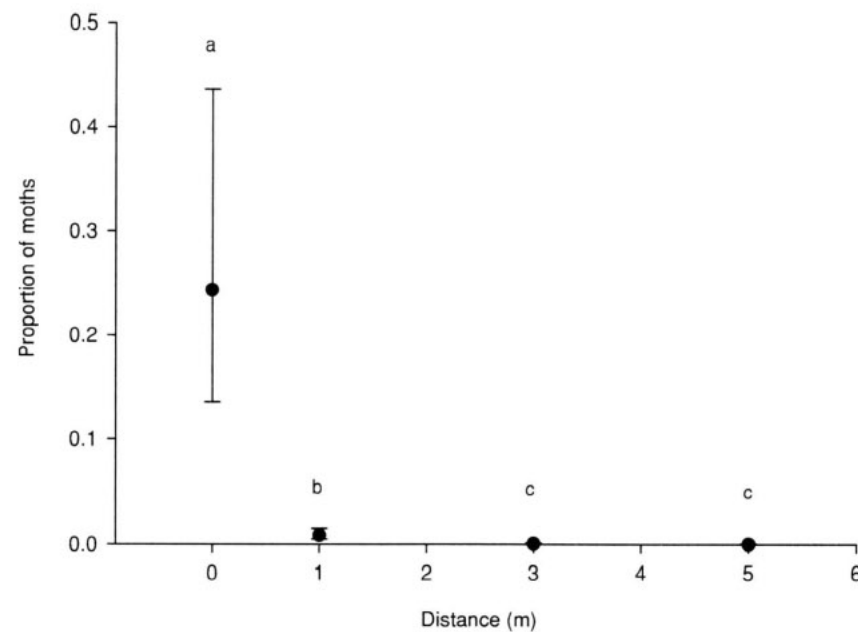

Fig. 1. Mean ($\pm$ SE) proportion of nightly western spruce budworm moth (open symbols) and bat (closed symbols) activity relative to sunset (bat and moth symbols are offset for ease of visual comparison).
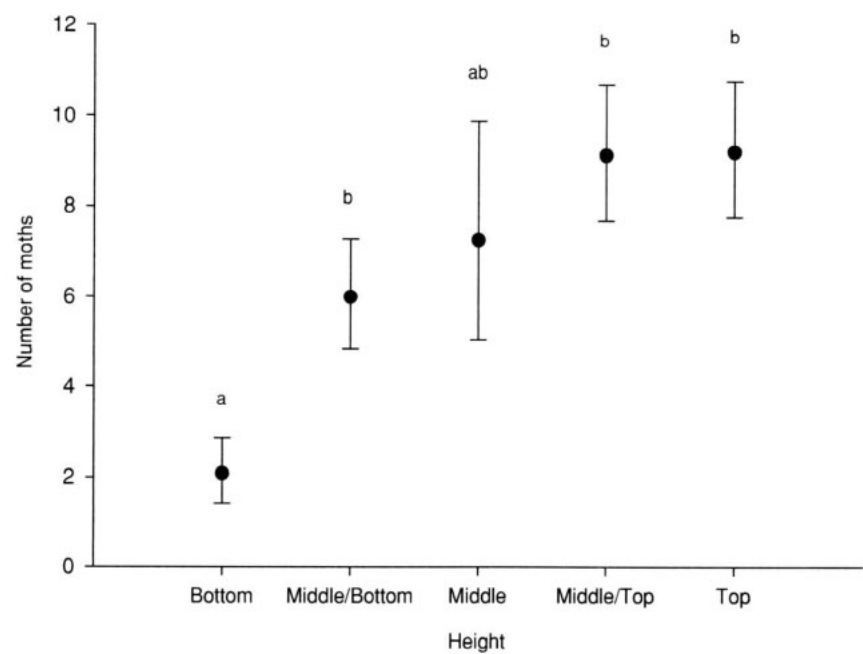
Fig. 2. Least square mean ($\pm$SE) proportion of western spruce budworm moths observed in 1-min intervals at different distances from the base of trees. Means with different letters are significantly different, $p < 0.05$. Means and standard errors were back-transformed from logged values, thus resulting in asymmetrical SE's and values that do not total to 1.0.

1, 3, or 5 m from the tree ($p < 0.001$ in each case; Fig. 2). Although numbers of moths varied with time of night ($F = 9.10$, $df = 3, 208$, $p < 0.001$), the pattern of activity with distance from the tree was the same at all times, whether before or after sunset.

Moths most often flew near the tops of trees. Once non-significant interactions were removed, the ANCOVA model analyzing variation in height of moths, contained minutes relative to sunset, tree number, and height within the tree as main effects, and ambient temperature as a covariate. The model explained a significant amount of variation in the number of budworm observed ($F = 7.79$, $df = 29, 148$, $p < 0.001$). The number of moths varied with height ($F = 7.05$, $df = 4, 148$, $p < 0.001$); there were more moths at the top of the tree than at the bottom (Fig. 3).

Although individual moths ($N = 68$) varied greatly in their behavior, on average they spent most of their time flying (mean $57.5 \pm 4.9\%$ SE). The ANCOVA model analyzing variation in time spent in flight contained time relative to sunset and the total observation time as main effects, and ambient temperature as a covariate. The model explained a significant amount

Fig. 3. Least square mean ($\pm$ SE) number of western spruce budworm moths observed flying at different heights in trees during 1-min periods. Means with different letters are significantly different, $p < 0.05$.

of variation in time in flight ($F = 6.24$, $df = 3$, 64, $p < 0.001$). The time spent in flight varied with the total amount of time observed ($F = 6.54$, $df = 1$, 64, $p = 0.013$) and with ambient temperature ($F = 4.22$, $df = 1$, 64, $p = 0.044$). There was no significant difference in flight time before sunset versus after sunset ($p = 0.91$).

Both before and after sunset, moths flew primarily 'back and forth', perpendicular to the tree branches. They also flew in small circles or parallel to the branches. During flight, individuals frequently touched the branches for a fraction of a second and then continued flying. These touch-downs were mostly on the tips of the branches.

A χ^2 test on the sweep-net data for male and female moths flying near trees showed that significantly more male moths ($N = 76$) than females ($N = 9$) were flying, both before and after sunset ($\chi_c^2 = 52.82$, $df = 1$, $p < 0.001$).

While sitting on the vegetation, moths remained stationary most of the time (91.1%) and rarely fluttered their wings (1.2%) or crawled (7.7%).

The proportion of moths crawling before sunset was not significantly different from the proportion after sunset ($\chi_c^2 = 0.32$, $df = 1$, $p = 0.57$). However, there was a significant difference in the proportion of individual moths which fluttered their wings, with more fluttering before sunset than after sunset ($\chi_c^2 = 4.42$, $df = 1$, $p = 0.036$).

DISCUSSION

Earless moths have evolved behaviors that help to reduce predation by bats. This may be accomplished by changing the timing of flight resulting in temporal isolation, through different use of space to yield spatial isolation, or by altering certain behaviors such as flight style or wing fluttering to decrease cues that predators might use (Fullard, 1998; Rydell, 2004).

Western spruce budworm activity was not completely temporally isolated from that of foraging bats in our study area. Although at least some moths became active before sunset and thus before bats were active, the peak in moth activity was approximately one hour after sunset, when bats were foraging. This agrees with laboratory observations (Edwards, 1962). It may be that predation from visually hunting, diurnal avian predators exerts selection favoring crepuscular activity. None-the-less, western spruce budworm moths were active much earlier in the evening than some other species of moths that have been studied (e.g. Edwards, 1962; Acharya, 1995; Rydell *et al.*, 1996) and as a consequence likely faced lower predation from bats than if all of their activity occurred after sunset. Even amongst earless moths, this is unusual behavior (Fullard and Napoleone, 2001), although at least one congeneric species (*Choristoneura fractivittana*) is also crepuscular in its activity pattern (Fullard and Napoleone, 2001).

To a certain extent, western spruce budworm may be spatially isolated from bats because the moths are most active close to their host trees. This is consistent with previous observations of western spruce budworm moths primarily flying close to trees and not between trees (Sower and Daterman, 1985). This behavior is exhibited especially by male moths responding to pheromone signals from females on branches (Sower and Daterman, 1985). While this spatial distribution may be motivated primarily by mate-finding, it also may be effective in reducing predation from bats because of the cluttered environment trees present to bats, both physically and in terms of detection. Echoes from background foliage hide the echo from insects, a phenomenon termed "acoustic crypsis" (Rydell, 1998). Insects can achieve acoustic crypsis by flying close to vegetation. Aerial-hawking bats do not usually have this clutter-detection problem because background echoes are reduced or even absent when prey are flying in open air. Clutter is more of a

problem for gleaning bats, such as some *Myotis* species, because they need to detect prey amongst an irregular background which can result in prey echoes that are obscured by echoes from the background. Detection of the target is more difficult (Faure and Barclay, 1994). Foraging bats not only have difficulty detecting prey in cluttered environments, they may have difficulty capturing them. For example, *Eptesicus nilssonii* detect moths within the clutter created by tall grass, but only capture moths when they fly above the grass. The dense grass poses a limitation to flight and maneuverability but not to actual detection (Jensen *et al.*, 2001). The type of spatial isolation we observed for western spruce budworm moths may not defend them against all bats. *Myotis evotis* in southern British Columbia catch insects close to foliage and frequently glean prey from vegetation (Fenton *et al.*, 1980; Wilson and Barclay, 2006).

Moths could be spatially isolated from bats in the vertical axis as well as the horizontal. If moths are more active at heights where bats are not active, then this should result in decreased predation risk. Indeed, moth flight low to the ground and with an erratic style has been suggested to be an adaptation that reduces bat predation (Fullard and Napoleon, 2001). Eratic, low-altitude flight is more evident in earless moths than in eared moths and can decrease successful captures by bats (Lewis *et al.*, 1993).

Our data indicate that *C. occidentalis* do not fly low to the ground. Western spruce budworm moths were most active around the upper third of their host trees. The canopy may be the easiest area of the tree for bats to forage around, since it presents the least dense area of vegetation. Indeed, *E. fuscus* in southern British Columbia forages around the canopy, while *M. volans* forages from 10 m above the ground to the canopy top, and *M. lucifugus* and *M. yumanensis* forage from approximately 1 m above the ground to the canopy top (Fenton *et al.*, 1980).

Western spruce budworm moths may be most active in the tops of trees because food for their larvae is most abundant at this height. Females prefer to lay eggs in the crown of host trees; the density of western spruce budworm egg masses is highest in the upper third of trees and lowest in the lower third (Campbell *et al.*, 1984). The density of egg masses is also seven to eight times greater on taller trees than average height trees (Campbell *et al.*, 1984). If female moths are more likely to be higher in the trees, males actively searching for females are more likely to be found there as well. Therefore, the benefits of flying at tree-top height in terms of survival of young and finding a mate may outweigh the costs of increased bat predation.

Dispersal may be another phase of the life cycle of western spruce budworms during which they are vulnerable to attack by bats. Dispersal peaks within the first hour after sunset (Greenbank *et al.*, 1980), when the risk

of predation by bats is high. It starts with an upward flight from the upper crown of the trees, thus helping to explain the large number of individuals we observed high in the trees. Individuals rise high above the canopy and are then carried downwind, with the maximum density of dispersers occurring 100 m or more above the ground (Greenbank *et al.*, 1980). This is much higher than most bats forage (e.g. Fenton *et al.*, 1980), reducing the predation risk. While both male and female western spruce budworms disperse, the majority (61–91%) are females carrying eggs (Greenbank *et al.*, 1980). Thus, although our captures indicated that, close to the vegetation and the ground, male western spruce budworm moths are more exposed to predation than females are, at the tops of trees and away from vegetation, females may be more at risk to predation by bats, at least early in dispersal before they reach high altitudes.

The erratic flight of western spruce budworm moths that we observed has been noted before (Sower and Daterman, 1985). Males fly close to tree branches and with a wandering pattern, a classic anemotactic response to pheromone release (Sower and Daterman, 1985). While this may be a response to the pheromone trails of females, the erratic flight may also reduce the predictability of their flight and the vulnerability of the moths to aerial hawking bats.

Aerially hunting bats likely impose the greatest predation pressure on western spruce budworm moths, given their diversity and abundance. However, gleaning bats such as *M. evotis* present a different predation pressure. *M. evotis* is able to detect the movement and sound of fluttering and crawling insects through passive audition (Faure and Barclay, 1994). Some species of moths flutter their wings to warm their flight muscles (Heinrich and Bartholomew, 1971), but western spruce budworm moths rarely fluttered their wings or crawled while they were on branches, and females do not flutter their wings to disperse pheromones (Sanders and Lucuik, 1972). Moths fluttered less after sunset, when bats were foraging, than before, and this lack of movement may reduce their detectability to gleaning bats. Some moths with ears stop moving when they detect an echolocating bat (Werner, 1981; Acharya and McNeil, 1998; Jones *et al.*, 2002), and reduced movement by moths without audition may be an important anti-predator adaptation.

Western spruce budworm is an outbreak species and during the peak in the outbreak cycle, the point at which we conducted our study, predator swamping may reduce the per-capita predation risk (Hamilton, 1971). The relatively synchronous emergence of adult moths, in combination with high densities during the outbreak peak, may be effective in this way, as has been suggested for other synchronous species of moth (Lewis *et al.*, 1993). However, during periods of low western spruce budworm abundance, swamping would be less effective and other defenses are presumably more important.

Most large-bodied moths have ears and rely on audition as their primary defence against echolocating insectivorous bats (Rydell, 2004). In some species, audition considerably reduces an individual's vulnerability to bats (e.g. Roeder, 1967; Acharya and Fenton, 1999). Although western spruce budworm moths do not detect echolocating bats, they have behaviors that likely reduce their vulnerability to both aerial and gleaning bats. The effectiveness of these behaviors remains to be determined, however, as does their importance during non-outbreak conditions when swamping of predators is less likely.

ACKNOWLEDGEMENTS

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