Odonatologica 33(2): 169-179 *June 1, 2004*

HABITAT SELECTION AND POPULATION PARAMETERS OF *SYMPETRUM INFUSCATUM* (SELYS) DURING SEXUALLY MATURE STAGES IN A COOL TEMPERATE ZONE OF JAPAN (ANISOPTERA: LIBELLULIDAE)

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Received September 1, 2003 / Revised and Accepted October 30, 2003

The mark-and-recapture method was used to study the population parameters of sexually mature adult *S. infuscatum* in a forest-paddy field complex in the cool temperate zone of Japan. After emergence, they moved into the forest gaps, and they remained and fed exclusively in the forest gaps throughout their lives. Mature ♂♂ captured outnumbered mature ♀♀ on each sampling day in the paddy fields, but not in the gaps. However, the estimated daily numbers in both habitats and/or the whole survey area roughly indicated a 1:1 sex ratio. The estimated daily survival rates and daily immigrations showed that ♀♀ were apt to stay in the forests, while ♂♂ sometimes dispersed, though ♀♀ in the paddy fields tended to have a long-range flight. In the morning, some of the paired couples flew to the paddy fields in tandem and oviposited on the wing; these were so-called flyers. The rest remained in the forests the entire day; these were designated as perchers. The forest gaps were thus important for the life cycle of this species both as feeding and roosting sites.

INTRODUCTION

In most dragonfly species, daily movement in search of food, mates, and roosting sites is a fundamental process that influences the dynamics of spatially divided populations (e.g., JONSEN & TAYLOR, 2000). Although maiden flight often takes an individual far from its site of emergence (CORBET, 1999), the daily movements of adults arise from diurnal behaviour in response to differences in the potential roosting, mating and ovipositing sites of different habitats.

For many *Sympetrum* species in Japan, rice paddy fields are the main habitat for the larval stages. After emergence, tenerals generally embark on a maiden flight, leaving the paddy fields. A number of studies have revealed that the sexually immature period of adults is usually the principal period of odonate dispersal (e.g., MICHIELS & DHONDT, 1991), and many species fly a considerable distance away from water (CORBET, 1999), implying that sexually mature adults return and tend to stay by the water. Among *Sympetrum* species, *S. frequens* and *S. pedemontanum* represent two extremes of maiden flight behaviour. Individuals of *S. frequens* move far from the paddy fields to the mountains, remain in the mountains over the hot summer season, and return to the paddy fields in autumn (TANAKA, 1985; TSUBUKI, 1987; MIYAKAWA, 1989). *S. pedemontanum*, on the other hand, exhibits a short maiden flight, if any, and remains almost exclusively in the paddy fields (TAGUCHI & WATANABE, 1985). Other *Sympetrum* species, including *S. infuscatum*, display maiden flight behaviours intermediate between the two. Generally, they enter into forests or woods near the paddy fields, and stay there throughout their immature stages. After sexually maturation, many *Sympetrum* species return to the paddy fields for reproduction, while *S. infuscatum* remains mainly in the forest gaps.

S. infuscatum is a so-called "flyer", i.e., the mature adults of this species fly over the paddy fields at relatively high velocity and lay eggs in tandem on the wing. Like migratory species such as *S. frequens*, there seem to be no physical limitations in paddy fields for adult behaviour. The maiden flight is usually long, and the individuals probably disperse during their adult stages. Accordingly, it is difficult to clarify the population parameters of a flyer species, both because of the difficulty of initially capturing individuals in the paddy fields, and because of the difficulty of recapture (CORBET, 1999). Therefore, little attention has been paid to the population ecology of such species, though the partial life history and occasional observations have been reported (e.g., ISHIDA, 1969). Using the mark-and-recapture method, WATANABE & TAGUCHI (1988) clarified the population structures of seven *Sympetrum* species in autumn paddy fields, although no *S. infuscatum* adults in the mature stages were recaptured. However, our initial observations in the survey area indicated that a considerable number of males and females in both the sexually immature and mature stages spend the day perching in the forest gaps: these individuals are thus known as "perchers". Thus, dragonflies vary in their abilities or propensity to move over the different types of habitat, which might have broader-scale consequences for population dynamics.

The aim of the present study was to obtain quantitative information on the adult population parameters of *S. infuscatum*. More than 20 researchers were employed to estimate the mature adult population size and daily movements using the mark-and-recapture technique. Reproductive behaviour was also observed during the experiments, which contributes towards our knowledge of the *S. infuscatum* mating system.

SPECIES AND STUDY AREA

Populations of *S. infuscatum* were studied in an isolated plain of the Kamishiro region in Shirouma, Japan in 2000-2001. The plain lies in a cool temperate zone at an elevation of 750m (Fig. 1). The plain is composed

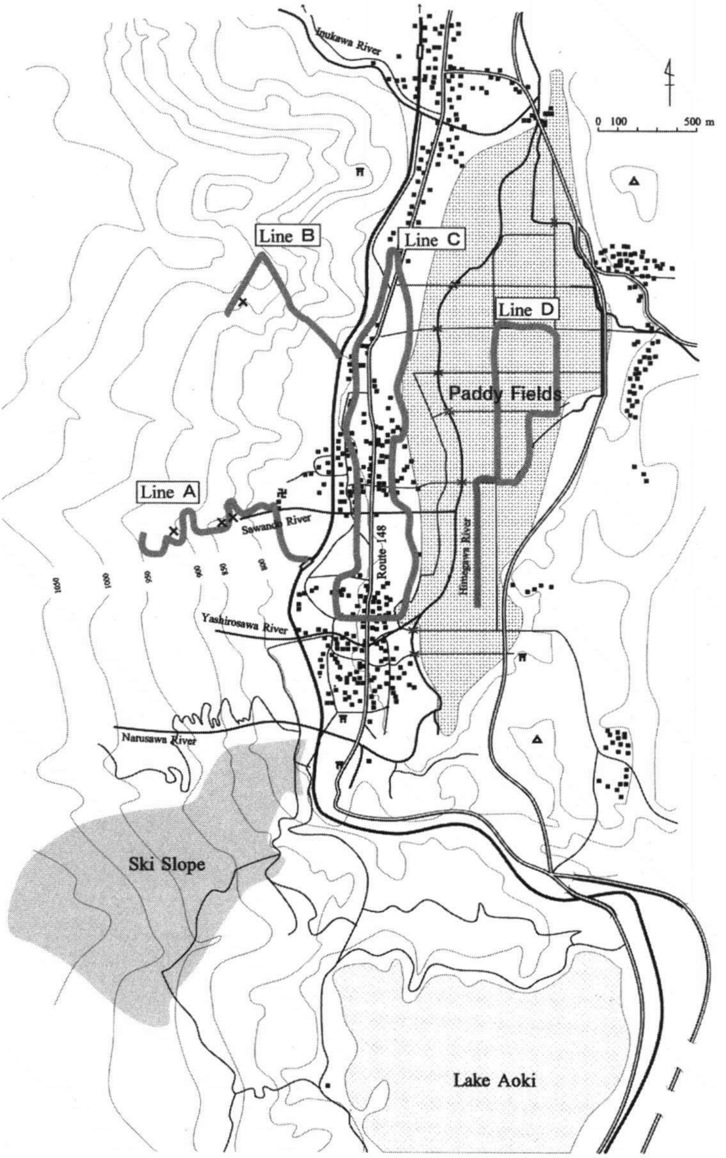

Fig. 1. Map of the study area, Kamishiro, Shirouma, Nagano Prefecture. – Lines (A-D) represent the survey lines of the *S. infuscatum* population for the mark-recapture method. Shaded areas show paddy fields, and villages are indicated by the aggregation of small black squares that represent houses and buildings.

of rice paddy fields (ca 2 km^2) and villages surrounded by hills or mountains with coniferous (cedar) forests. Rice reaping in the paddy fields is carried out annually in early October.

S. infuscatum is a non-territorial dragonfly. Sexually mature adults were found in the plain in the morning from late August to mid-September. Once pairs were formed in the surroundings of the paddy fields, which are located in the centre of the plain, they may have flown immediately to the paddy fields, or may have come from a greater distance. In the mating of this species, the male retains hold of the female and the pair flies over the paddy fields in tandem and lays eggs on the wing above the rice plants. Lone females do not oviposit. After oviposition, the pair separates and the dragonflies return to the gaps in the cedar forests, where a considerable number of adult *S. infuscatum* perch throughout the day to forage or escape from birds and other predators, but there is little competition for perching sites among them. No mature adults show mating behaviour.

METHODS

We studied the *S. infuscatum* population using the mark-and-recapture method in the plain and the forest gaps. Although the survey area was large, the habitat is roughly isolated. We patrolled along the pass (total 7 km) in gaps and paddy fields over an area on a day in late August, when most of the adults had matured.

Adult censuses were carried out along 4 survey lines simultaneously in the survey area on mostly clear days for 5 days and 11 days in late August of 2000 and 2001, respectively, during which time the *S. infuscatum* population was considered to be stable and reproductive activity was high in the paddy fields. It took about 4 hours to intensively patrol each survey line. As shown in Figure 1, survey lines A (ca 900 m) and B (ca 900 m) followed an upsloping path that included many gaps in the cedar forests. The survey line C (ca 3000 m) was located in the villages and the line D (ca 2000 m) was in the paddy fields. Plants in the survey lines were occasionally trimmed by residents and farmers. Consequently, vegetation along the lines was less than 30 cm tall, and the approximate perching height of *S. infuscatum* in the gaps was usually less than 1 m. However, in the paddy fields, the height of the ovipositional flight in tandem was about 1.5 m, or 10-20 cm above the rice plants, while that of movement flight in tandem was more than 2 m.

All adults detected were captured with a net and mapped. Each was given an individual number that was marked with a black colour felt-tipped pen on the undersurface of the left hind wing. They were released immediately at the same capturing site after recording the date, site name, sex, and age. The marking was considered to have only minor effects on their flight activities (and the probability of predation) because most adults began to fly normally soon after marking. Adults wounded during marking were treated as dead individuals in the calculations. Although the age of sexually mature *S. infuscatum* was estimated according to four age classes, mainly by body colour and wing condition, as in the case of the other dragonfly species (e.g., McVEY, 1985; WATANABE & HIGASHI, 1989), in late August the majority of adults were in the early mature stages. There were no old mature adults.

In most dragonfly populations, the recapture probabilities of the two sexes were different (e.g., WATANABE & HIGASHI, 1989). The sexes of *S. infuscatum* were processed separately through Jolly's analysis (JOLLY, 1965).

RESULTS

Most males captured were mature individuals, judging from the dark red colour of the abdomen, and most females were also mature based on their brown red colouration. Adults were found throughout the entire habitat, but males were sometimes concentrated on the margins of forests or on a hedge in the village in the late afternoon and the evening, both of which were sunlit areas. Observations during the mark-and-recapture sampling (M. Watanabe & H. Matsuoka, unpublished) showed that both sexes perched on the tips of twigs or grass blades in forest gaps, and made intermittent feeding flights, after

Table I
Total number of adults marked in forest gaps and in paddy fields during the course of the survey (5 days for 2000 and 11 days for 2001)

	2000		2001	
Habitats	males	females	males	females
Forest gaps	1,449	1,565	4,201	3,791
Paddy fields	1,863	603	4,046	1,417

which they usually returned to the same perch. In addition, there were few interactions among them, i.e., there was no courtship behaviour, no mating behaviour, no territorial behaviour, and so on. Forest gaps provide good sources of food for adults. The total number of adults captured in gaps indicated that the sex ratio was near unity in both 2000 and 2001, though the number of sampling days was different in each year (Tab. I). On the other hand, most adults in the paddy fields flew continuously without landing; all females captured were in tandem, but there were a considerable number of single males. Consequently, the number of males captured in the paddy fields was about 3 times that of the females in both 2000 and 2001. Since few single males were captured in the early morning, when there were many couples found flying in tandem over the paddy fields, and since the number of single males increased with time, the single males in the paddy fields appeared to be those males remaining after the separation of tandem couples. Single females appeared to return quickly to the gaps after oviposition.

The number of recaptured adults was too small to estimate the population parameters with a small standard deviation. In 2000, 31 males and 28 females were recaptured, or 0.9% and 1.3% of total number of adults released, respectively. By Jolly's method, there were 10,000 males in the gaps and 25,000 males in the paddy fields, and 33,000 females in the gaps and 20,000 females in the paddy fields.

In 2001, the number of recaptures increased 1.5-fold for both sexes, probably due to

Table II
Daily population parameters of adults estimated using Jolly's method (±SD)

Year	Sex	Parameters	Whole area	Forest gaps	Paddy fields
2000	♂	number	36,843±12,328	9,453±7,530	25,174±13,226
		survival rate	0.30±0.22	0.27±0.25	0.41±0.16
		number of immigrations	26,381±4,916	6,851±7,588	19,402±10,130
	♀	number	26,559±26,822	33,788±28,520	20,433±17,933
		survival rate	0.66±0.40	0.64±0.42	0.78±0.42
		number of immigrations	29,270±62,686	16,950±36,204	10,277±18,922
2001	♂	number	19,061±4,167	10,664±3,679	11,606±3,250
		survival rate	0.40±0.12	0.45±0.13	0.40±0.12
		number of immigrations	45,844±97,257	10,206±11,644	261,402±775,094
	♀	number	28,091±7,528	17,989±5,057	7,994±3,919
		survival rate	0.66±0.08	0.67±0.09	0.65±0.11
		number of immigrations	61,031±159,159	32,115±79,941	29,896±77,199

the long survey period, and then the standard deviation decreased. The daily estimated number of adults in the whole survey area, forest gaps, or paddy fields varied for both sexes, but the variance was larger for females than males. Assuming that the sex ratio was 1:1, we calculated the whole daily population by doubling the number of males, to 70,000 in 2000 and 40,000 in 2001. In addition, Table II shows that half of the males were in gaps in daytime, and the number of females that remained in the gaps was twice the number of females that remained in the paddy fields in both years.

The change in estimated daily survival rate fluctuated in both sexes and habitats between 0.27 and 0.78 in 2000, and between 0.40 and 0.67 in 2001 (Tab. II). Both sexes co-existed in the same habitats, and gender seemed to have no effect on the survival during the survey period. No avian predation was observed in either sex. However, the estimated daily survival rate was low, particularly in males. Since the longevity of *S. infuscatum* is usually more than 2 months, this daily survival rate may be a reflection of the daily emigration rate from the survey area rather than actual mortality. SCOTT (1973) pointed out that Jolly's "survival" estimates should be closely correlated with residence for wild insect populations. In the present study, males in both gaps and paddy fields were more apt to emigrate than females. In addition, because the paddy fields were open habitats in which pairs flew about in tandem, the immigration and emigration rates of adults in the *S. infuscatum* population should be very high.

The movement between or among habitats was examined for recapture data in 2001 (Tab. III). For males, 61 movements were gap-to-gap, 16 were gap-to-paddy fields, 11 were paddy fields-to-paddy fields, and 15 were paddy fields-to-gap. On the other hand, out of 73 movements observed in females, 58 were gap-to-gap, indicating that females were more apt to stay in gaps than males (G = 9.2676, 0.05>p>0.01).

From the mark-and-recapture data obtained among the study sites, the average distance of flight for adults was calculated as shown in Table IV. Since the adults were not always recaptured the day after being released, the individual distances per day calculated did not coincide with the actual distances of flight trajectory. Furthermore, the survey period was different each year. However, the mean distance per day between capture and recapture sites throughout the whole area was similar in both years for both males and females, and males showed significantly higher activities than females in 2001.

Table III

Release and recapture sites with duration after release in 2001

Sex	Direction	Number of adults	Days after release (±SD)	Max. days
♂	Gaps → Gaps	61	2.0±1.4	5.5
	Gaps → Paddy fields	16	2.5±1.7	5.0
	Paddy fields → Gaps	11	4.1±3.2	8.5
	Paddy fields → Paddy fields	15	2.0±2.1	6.5
♀	Gaps → Gaps	58	2.1±1.7	9.0
	Gaps → Paddy fields	7	2.0±1.5	4.5
	Paddy fields → Gaps	2	2.3±0.4	2.5
	Paddy fields → Paddy fields	6	2.1±2.3	6.5

Within forest gaps, both sexes showed low rates of movement activity. The rate of less than 100

Table IV

Distance of mean daily movement (m/day, ±SE); – in parentheses (): number of adults

Year	movement	♂	♀		
2000	throughout the survey area	259.3± 70.4 (26)	101.2± 35.0 (27)	U=292.0	P=0.130
2001	throughout the survey area	231.2± 40.1 (103)	145.7± 40.1 (73)	U=2982.0	P=0.016
	within gaps	187.9± 45.5 (62)	95.4± 35.3 (56)	U=1395.5	P=0.046
	between gaps and paddy fields	378.6±102.2 (28)	295.9± 87.1 (8)	U= 106.0	P=0.837
	within paddy fields	143.9± 41.0 (15)	479.7±211.4 (6)	U= 20.0	P=0.055

m/day for females indicated that females moved only to the next gap within a single day, and that females remained significantly more stable in gaps than males. Relatively few adults were recaptured in paddy fields after being released in gaps and vice versa. On the other hand, within paddy fields, females were recaptured at a greater distance from the release than males.

DISCUSSION

Our study revealed that *S. infuscatum* is not restricted to a whole survey area whether it shows low flight activity in forest gaps or high flight activity in paddy fields. The available methods do not allow us to trace migrations of great distance. However, some of our results coincided with the fragmental information reported by UEDA (1997), i.e., that this species always flies over the paddy fields in autumn. The high density of tandem flying in the paddy fields throughout the reproductive season suggests that this species does not exhibit territoriality, and little intraspecific aggression for perching sites in forest gaps was observed (M. Watanabe & H. Matsuoka, unpublished). Few *S. infuscatum* males were "opportunists" that flew about and searched for mates in the forests, and thus there were no pairs in the forest gaps. Tandem flying and copulation seemed to occur along the border between the forests and the paddy fields in early morning. Outside-pond pairing in formation has been reported in *S. parvulum* (UEDA, 1979) and *S. danae* (MICHIELS & DHONDT, 1989).

More than ten *Sympetrum* species that inhabit Japanese paddy fields have been recorded (ISHIDA, 1969). Some of them (e.g., *S. frequens* and *S. kunckeli*) were found in the present survey area. In late August most of these were sexually immature and considered to have been accidentally captured in the paddy fields, and very few adults were observed in the forest gaps. Therefore, no odonate species coexists with mature *S. infuscatum* in the survey area during late August. There were few *S. pedemontanum* individuals in the survey area, a species in which sexual maturation is reached the earliest among *Sympetrum* species (MICHIELS & DHONDT, 1987). Since the other *Sympetrum* species appear after mid-September, the maturation of *S. infuscatum* is the earliest in the survey area. WATANABE & TAGUCHI (1988) pointed out that the *Sympetrum* community of the paddy fields in early October consists of diverse species and individuals of diverse age, due to different duration of maturation after emergence.

Diurnal activity patterns, particularly on reproduction, in mature *Sympetrum* adults in the paddy fields have been well documented (KINOSHITA & OBI, 1931; ARAI, 1983; UEDA, 1979). CORBET (1980) stated that the male activity pattern at the water is a reflection of the arrival rate of receptive females. Particularly, in the species adopting territorial tactics, mature males return to water to establish territories, while mature females tend to visit only to oviposit (VAN BUSKIRK, 1987). Thus, the probability of recapture for territorial males is higher than that for females (CORBET, 1999). Consequently, such diurnal behaviour seems to lead to a male-biased operational sex ratio in the paddy fields as reproductive sites (e.g., WATANABE & TAGUCHI, 1988). In this study, however, more than half of the mature *S. infuscatum* females remained at forest gaps every day. Female arrival at the paddy fields depends upon male activity, since females were brought in in tandem by a male from the margins of the forests. Thus, the sex ratio in the paddy fields must be unity.

Although the flying *S. infuscatum* adults were harder to capture because they flew at the centre of the paddy fields or at more than 2 m above the rice plants, the sex ratios based on the estimated daily numbers for the two years of measurement appeared to be roughly 1:1, with a slight predominance of males. An equal sex ratio in the reproductive area was also reported for *S. pedemontanum*, which inhabits paddy fields without any flights away from the fields (TAGUCHI & WATANABE, 1985). In our study, however, only tandem pairs of *S. infuscatum* came to the paddy fields and started oviposition without delay. The surplus males captured must be the individuals delayed in their return to forest gaps after separating from a tandem pair following oviposition. Some of the lone males intermittently perched on the ground or the tip of rice blades, and these may have been waiting for the flight activities to resume. They have to pay high energy cost associated with tandem flight including oviposition in tandem in the paddy fields. TAGUCHI & WATANABE (1995) observed that males might withstand higher thoracic temperature in tandem flight than females. The other lone males flew about the paddy fields, as if searching for any stray receptive females that had separated from other males before oviposition, though we did not detect any difference in the aim of the flight behaviour of the single males in the paddy fields. MICHIELS & DHONDT (1991) reported that *S. danae* males readily remated on the same day whenever possible. McMILLAN (1996) separated *S. vicinum* tandem pairs and found that most females were immediately chased by lone males and taken into tandem.

The daily population density of *S. infuscatum* was high (2.25 and 1 adults per 100 m^2 of the paddy fields for 2000 and 2001, respectively), and the distribution of tandem pairings appeared to be roughly random. No mutual attraction among pairs was observed. The rice paddy fields supported the random distribution of the potential oviposition sites, where the females laid eggs in tandem on the wing. The same oviposition behaviour was observed in *S. darwinianum* (TAGUCHI & WATANABE, 1995), which also has little site preference for oviposition within the paddy fields. On the other hand, *S.*

pedemontanum, *S. frequens*, *S. eroticum*, and *S. vicinum* lay eggs in puddles before the patchily distributed water surfaces in the paddy fields dry up following the rice harvest, thus, these species must have strong preferences for oviposition sites within the paddy fields (KINOSHITA & OBI, 1931; MIZUTA, 1978; McMILLAN, 2000).

Both male and female *S. infuscatum* individuals that remain in the forest gaps generally use a sit-and-wait foraging tactic in order to catch prey throughout the entire day. HIGASHI (1973) observed the feeding behaviour of *S. frequens* in coniferous forests where there was an excess of females. Since no mating behaviour was observed in the hills, this habitat may be a feeding site, as well as, presumably, a roosting site. TAGUCHI & WATANABE (1987) suggested that females of *S. eroticum* visit the paddy fields only once every few days to mate and oviposit. MICHIELS & DHONDT (1991) also showed that in *S. danae* females each oviposition bout was usually followed by a non reproductive period of approximately 4 days. Therefore, in this study area, the large number of *S. infuscatum* females in the forest gaps might develop clutches of eggs cyclically, as suggested by FINCKE (1982).

In general, immature individuals of most dragonfly species fly away from water (MOORE, 1953), and it is considered that they disperse mainly by random movements during the maiden flight (e.g., JOHNSON, 1960; CORBET, 1999). Although the maiden flight plays a role in dispersal for both sexes of many odonate species, mature males also dispersed in the present study. Since all mature adults returned to the forest gaps, the latter must be the major habitat of *S. infuscatum*. Then, two-way movement between the forest and the paddy field needs to occur in both sexes for reproduction, indicating that they have the ability to switch between two distinct flying habits, i.e., percher and flyer habits.

Most odonate females are polygamous, although it has frequently been reported that they can refuse to copulate (CORBET, 1999). As in the case of *S. infuscatum* staying in the forest gaps, the high density seems to release mature males to attack or harass single females for the purpose of mating. However, in our study, all the adult males tended to simply perch, and did not interfere with the females. There must be an additional mechanism which prevents the release of unnecessary courtship behaviour, because perching females did not avoid males trying to perch at the same site in the forest gaps, as they did in the case of *S. danae* (MICHIELS & DHONDT, 1989). This is probably their lifetime habit as a percher in the forest gaps. Although further detailed behavioural study of this species is needed, our results make clear the importance of the forest gaps for the life history of *S. infuscatum*. It is apparent that dragonflies are good indicators of habitat types and of the ecological quality of the land-water-interface because of their complex habitat requirements (see review in CORBET, 1999). In the species studied, the effect of habitat fragmentation is not likely to lead to isolation effects. The abandoned forests have supplied a large number of gaps which are a major habitat for *S. infuscatum*. This fact further increases the indicator potential of the species in the forest-paddy field complex ecosystem and has an effect on the evaluation of conservation strategies.

ACKNOWLEDGEMENTS

We would like to thank H. TANI, T. MURAKAMI, K. HOSOI, Y. MIMURA, T. HIGASHI, Y. NAKANISHI, M. BON'NO, T. IMOTO, N. KATAYAMA, and K. FUTAMURA for their assistance in the field. The students of the Biological Science Club of Yaei-Higashi High School and the students of the Department of Natural Science, Faculty of Education, Mie University also helped. This work was supported in part by a grant to MW from the University of Tsukuba Research Projects.

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