

# Environmental Influences on Flight Activity of USDA-ARS Russian and Italian Stocks of Honey Bees (Hymenoptera: Apidae) During Almond Pollination

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**ABSTRACT** Differences in flight activity and in the percentages of pollen foragers between commercially managed honey bees, *Apis mellifera* L. (Hymenoptera: Apidae), of two stocks (USDA-ARS Russian,  $n = 41$  colonies; and Italian,  $n = 43$  colonies) were evaluated in an almond, *Prunus dulcis* (Miller) D. A. Webb, orchard in Kern Co., CA, during February and March 2002. Flight activity was measured by taking 1-min counts of bees exiting colonies on each of 9 d. Flight activity was best predicted with a model containing the effects of colony size (populations of adult bees and sealed brood), temperature, time of day, the interaction of adult bee population with temperature, and the interaction of adult bee population with time of day. Flight increased linearly with adult bee and brood population, had a quadratic relationship with temperature (increasing, but less so at higher temperatures), and had a quadratic relationship with time of day (decreasing, but less so at later times). Larger colonies had more response to changing temperatures and less response to different times of day than small colonies. Bee type had no direct influence on flight activity at any given colony size, temperature, or time of observation or when evaluated using a reduced data set retaining 34 Italian colonies and 32 Russian colonies whose mean sizes were equal. Overall, however, Russian colonies were less populous by about one-fourth and so fielded on average 71% of the foragers that Italian colonies did. Pollen collection was measured by capturing returning foragers on 4 d. The percentages of foragers with pollen were not different for the bee types.

**KEY WORDS** *Apis mellifera*, *Prunus dulcis*, pollination, foraging behavior

Selective breeding of honey bees, *Apis mellifera* L. (Hymenoptera: Apidae), that originated in eastern Russia recently has produced a stock that resists *V. destructor* Anderson & Trueman, a serious bee-keeping pest (Rinderer et al. 2001b). This Russian stock has been released by USDA-ARS to the bee-keeping industry (Rinderer et al. 2000) and is being used widely in the United States. In addition to resisting *V. destructor*, they resist infestation by *Acarapis woodi* (Rennie) (de Guzman et al. 2001) and have favorable honey production (Rinderer et al. 2001a).

To date, little is known about how newly developed honey bee stocks behave as crop pollinators. Verifying the suitability of Russian bees for commercial pollination is important because of the vital role honey bees play in crop production. Particularly important is the ability of honey bees to pollinate almonds, *Prunus dulcis* (Miller) D. A. Webb, on a commercial scale.

This crop involves the largest use of honey bees for pollination in the United States, involving at least one-third of the nation's managed colonies (Morse and Calderone 2000).

Almonds are a challenge to pollinate because bloom occurs very early in the year (typically late February to early March) when bee colonies have small populations and when bee flight may be hampered by cool weather. Suitable weather is thought to be the limiting factor in securing adequate pollination of almonds (Connell 2000).

The objective of this research was to compare Russian bees with Italian bees with regard to overall flight activity and pollen collection activity during almond pollination, and to predict flight activity according to genetic and environmental effects. Italian bees commonly are used for pollination because they have a tendency to produce populous colonies early in the season. Anecdotal reports from beekeepers have suggested that Russian bees fly more actively during cool conditions than other types of bees. Russian bees also have been reported to engage in more pollen collection; this is potentially significant, because pollen foragers are the most efficient pollinators of almonds (Thorpe 1996).

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## Materials and Methods

**Bees.** Seventy-two colonies each of commercially managed Russian bees and Italian bees were overwintered in 2001–2002 in south central Mississippi and northeast Arkansas, respectively. Colonies were managed similarly after being used for honey production in summer 2001. In preparation for winter, they were fed corn syrup, and they were medicated with fluvinate to control varroa mites and with oxytetracycline hydrochloride to control American foulbrood. Colonies had been started in spring 2001 with commercially reared queens. Russian queens were propagated from a select breeding line (OOB-716 [Green]); anecdotal reports by beekeepers suggested that bees of this line flew under relatively cool conditions. Russian queens mated in an area where all managed colonies had Russian queens for the previous 3 yr. The purity of these presumed Russian ♀ × Russian ♂ matings was determined by DNA fingerprinting after the field measurements. During almond pollination, colonies were housed in two-story, deep Langstroth hives, and the hives were kept on pallets (four colonies of one bee type per pallet).

The size of each colony was determined during 1–4 March 2002 by measuring the amounts of adult bees (as “frames of bees”) and sealed brood (as “cm<sup>2</sup> brood”) that existed just after full bloom in the almond orchard. The area of each comb covered by a single layer of adult bees was estimated to the nearest 0.1 comb (≈176 cm<sup>2</sup>) when air temperatures were ≈14–17°C (58–62°F), and there was little or no flight. The area of each comb containing sealed brood was measured using a grid overlay of 2.54-cm squares.

**Study Site.** In early February 2002, ≈2 wk before the start of almond bloom, the colonies were moved to a 419-ha almond orchard in the Central Valley of California near Firebaugh (western Fresno Co.). They were placed along two sides of a block of trees made up of 50% ‘Nonpareil’ and 25% each of ‘Carmel’ and ‘Price’. Overall, the trees in the test block had ≈10% open flowers on 22 February, they were at peak bloom on 28 February, and there was ≈90% petal fall on 7 March. Colonies were arranged in six “sets,” each set comprised six pallets (three pallets of each stock, with stocks intermingled randomly). Sets were ≈100 m apart, and pallets within sets were ≈2 m apart. Because of the crowding of colonies in this commercial pollination setting, we estimated drifting of bees between colonies of the two stocks by comparing the percentages of black (Russian) bees found in 60-bee samples taken from the broodnest (i.e., presumably nonflying resident bees) and from returning foragers of each colony. In Italian colonies, the percentage of black bees was identical for bees in the broodnest (26.4 ± 21.0 [SD]) and among the foragers (26.4 ± 14.8). In Russian colonies, there was an insignificant difference ( $t = 1.584$ ,  $df = 81.8$ ,  $P = 0.941$ ) in the percentages of black bees in the broodnest (80.0 ± 22.5%) and among the foragers (72.4 ± 22.0%).

Two types of temperatures were measured at 1-min intervals with HOBO dataloggers (model H08–00804,

Onset Computer Corp., Pocasset, MA) near each of the six sets of bees. We measured “black globe” temperatures; this measure integrates the effects of air temperature, solar radiation, and wind speed on a model of an organism, and is well suited for evaluating environmental influences on bee flight (Corbet et al. 1993). We shaped 10-mm-diameter black globes from black laboratory stoppers. A hole was drilled to the center of the globe, and the end of a thermocouple (HOBO model TMC6-HB) was embedded there. Black globes were positioned in full sun at 1-m elevation. At the same locations, we also measured air temperature with a plain thermocouple under a shade cover. Mean temperatures from the six sites were averaged to get black globe temperatures and air temperatures associated with each minute that flight counts were made.

**Foraging Activity Counts.** Flight cones (Gary 1967) were used by two observers to obtain 1-min counts of the bees exiting colonies. One to three counts were taken from all 144 colonies on each day of observation. Because a single count took the two observers ≈2.5 h to complete, the colonies were measured in random order so that observations of each colony were distributed across a wide range of temperatures and times from day to day. Flight was measured daily on all colonies on 22–28 February and 6–7 March. On one occasion, we noted an apparent orientation flight involving hundreds of bees flying in a zig-zag pattern near the hive entrance; this count was excluded from the overall analysis of 840 flight counts.

**Pollen Foraging Rates.** Pollen collection was measured in one-half of the colonies of each bee type by randomly capturing 60 foragers returning to each hive between 1000 and 1400 hours on each of 4 d (26–27 February and 3–4 March). The percentage of bees carrying pollen was recorded, and afterward the bees were released.

**DNA Identification.** Because of possible misclassification of Russian colonies caused by mismatings of Russian queens to non-Russian drones and through queen supersedesures, final colony identification was made by DNA analysis. Colonies were sampled in the field on 4 March by collecting a group of worker bees at random from two combs within the broodnest. Samples were stored frozen until processing. The basis for the techniques used for DNA identification are given in Sylvester (2003). Briefly, DNA was extracted from thoraces of individual bees, and intersimple sequence repeat (ISSR) fragments of the microsatellite-primed DNA (primer UCB 881) were amplified by polymerase chain reaction and digested with the restriction enzymes AseI, HhaI, HpaII, and SspI. ISSR-restriction fragment length polymorphism fragments were visualized using ethidium bromide after electrophoresis in horizontal-slab gels. The fragments from the four digestions when used together allow group assignments as Russian or non-Russian (H.A.S., unpublished data). In this experiment, colony classifications were based on identifying two bees per colony at these probabilities. This resulted in classifying 41 colonies as Russian and 43 colonies as Italian (i.e.,

**Table 1.** Results of analysis of variance (type 3 tests from GLM) and parameters for regression equations that describe the influences of bee type, temperatures, broodnest size, adult bee population, and time of day on honey bee foraging activity during almond pollination

Predictor variable	F	df	P > F	Parameter estimate	SE
Bee type <sup>a</sup>	0.49	1,750	0.483	I, -148.85 R, -152.47	37.29 36.83
Temp	124.01	1,750	<0.001	28.56	2.56
Temp <sup>2</sup>	130.37	1,750	<0.001	-0.61	0.05
Broad population	37.46	1,750	<0.001	0.14	0.02
Adult bee pop	19.85	1,750	<0.001	13.68	3.07
Time of day	23.52	1,750	<0.001	-27.57	5.69
Time of day <sup>2</sup>	23.36	1,750	<0.001	1.08	0.22
Bees*time of day	54.78	1,750	<0.001	-1.54	0.21
Bees*temp	28.30	1,750	<0.001	0.64	0.12

The factors listed are those that remained after nonsignificant regressor effects were removed from the model. Parameter estimates are for colonies of all sizes; estimates for large and small colonies are not shown.

<sup>a</sup> Bee type is a classification effect and allows for different intercepts for each type in the regression equation. The parameter estimates are the intercepts for each type.

non-Russian), with all other samples being intermediate or indeterminate. The data from only these 84 colonies (of which 23 Russian and 19 Italian had been measured a priori for pollen foraging) were used in statistical analyses of flight activity and are presented here.

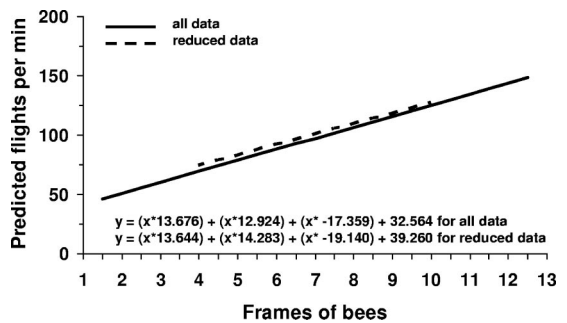
**Statistical Analyses.** We used a split-plot treatment structure with colonies within bee type as the main unit and with repeated measures of colonies through time as the subunit. Preliminary analysis showed no effects from placement of colonies along either side of the orchard or within sets of pallets; bee type and environmental effects therefore were evaluated in a completely randomized design. Analysis of variance (ANOVA) and regression analysis were used to evaluate the influence of bee type and environmental factors on flight activity. The full model analysis (PROC MIXED, SAS Institute 2000) evaluated the main effects of bee type, temperature, adult bee population, brood population, and time of day plus squares of effects and all two-way interactions. A term for time of day was added because it seemed in the field that bee flight decreased later in the day, despite temperatures being favorable. Factors found to be highly significant ( $P < 0.001$ ) were retained in the reduced model and then used as regressor variables to predict the number of bees leaving a colony under defined environmental conditions. Differences between the bee types in colony size parameters and in pollen collection on each day were evaluated with *t*-tests.

**Results**

Three general factors—colony size (both adult bee population and brood population), temperature, and time of day—were highly significant predictors of the flight activity observed in the 84 experimental colonies. The best explanation of flight activity occurred with a model that included the fixed effects of adult bee population, brood population, black globe temperature, the square of black globe temperature, time of day, the square of time of day, and the interactions of adult bee population with temperature and with time of day (Table 1). When these environmental

factors were held constant, flight activity was not significantly influenced by bee type ( $F = 0.49$ ;  $df = 1,750$ ;  $P = 0.483$ ). Intercepts of the response lines for the bee types (generated from regression equations of predicted flight) did not differ (Table 1). There were no interactions of the effect of bee type with those of colony size, temperature, or time of day, indicating the response lines for the bee types had parallel slopes.

Flight activity increased linearly with larger populations of adult bees and brood (Figs. 1 and 2). The predictive equations showed that a colony of the mean size (6.82 frames of adult bees and 1,484 cm<sup>2</sup> brood) issued 98 foragers per minute when other environmental factors were at their average values. Given otherwise average conditions, there was a 3.2-fold range in flight activity across the range of adult bee populations (1.5–12.5 frames of bees) measured in the test colonies (Fig. 1). Each additional frame covered with adult bees yielded ≈9.2 more bee flights per minute. There was a 2.3-fold range of flight activity across the range of brood populations (135–3,813 cm<sup>2</sup> of brood) in the colonies (Fig. 2). An additional com-



**Fig. 1.** Predicted effect of the size of the adult bee population on flight activity of honey bee colonies during almond pollination. Responses were modeled by using regression parameter estimates and the averages for broodnest size (1484 cm<sup>2</sup>), temperature (20.10°C) and time of observation (11:15 h). The reduced set retains subsets of colonies of the two bee types that had equal adult bee populations of ≈6.7 frames of bees.

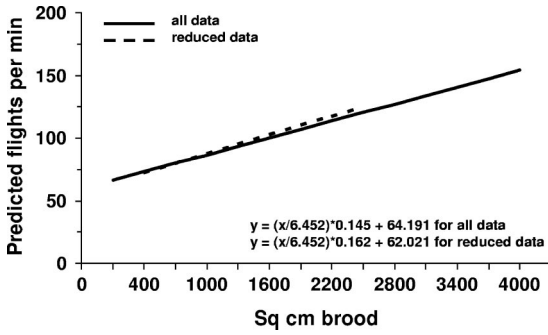


Fig. 2. Predicted effect of the size of the broodnest on flight activity of honey bee colonies during almond pollination. Responses were modeled by using regression parameter estimates and the averages for adult bee population (6.82 frames of bees), temperature, and time of observation. The reduced data retains subsets of colonies of the two bee types of equal size (as in Fig. 1); these colonies on average had  $\approx 1,510 \text{ cm}^2$  of brood.

plete frame of brood ( $1,770 \text{ cm}^2$ ) yielded 39.6 more bee flights per minute.

Because the effect of adult bee population size (but not brood nest size) interacted with effects of temperature and time of day, we present results for temperature and time when grouped for “large” colonies (those with  $\geq 6.82$  frames of adult bees, mean 9.30) and “small” colonies ( $< 6.82$  frames of bees, mean 4.77). Flight activity showed a quadratic response to black globe temperature when the other environmental factors were held constant. Activity increased with rising temperature (Fig. 3). The influence of temperature on flight activity was greater for large colonies than for small colonies. The predictive equations for large and small colonies both indicated a minimum temperature threshold for flight of  $12\text{--}13^\circ\text{C}$  ( $\approx 53^\circ\text{F}$ ) and maximum activity at  $26.5\text{--}27^\circ\text{C}$  ( $\approx 80^\circ\text{F}$ ). At this maximum, small colonies exhibited only 59% of the flight activity that large colonies had. Black globe temperatures ex-

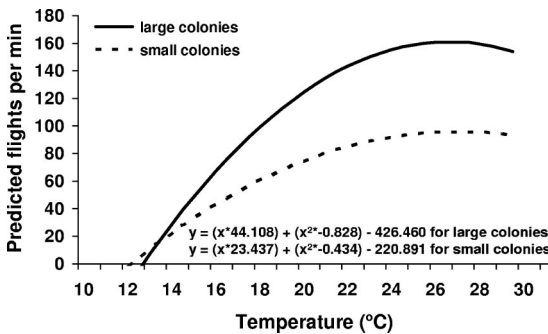


Fig. 3. Predicted effect of black globe temperature on flight activity from large ( $\geq 6.82$  frames of bees) and small ( $< 6.82$  frames of bees) colonies of honey bees. Responses were modeled by using regression parameter estimates and the averages for broodnest size (large,  $1,748 \text{ cm}^2$ ; small,  $1,258 \text{ cm}^2$ ) and time of observation (large, 11:14 h; small, 11:15 h).

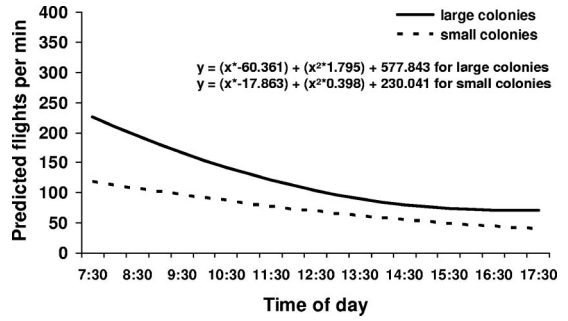


Fig. 4. Predicted effect of time of day on flight activity from large and small colonies of honey bees. Responses were modeled by using regression parameter estimates and the averages for temperature (large,  $20.15^\circ\text{C}$ ; small,  $20.06^\circ\text{C}$ ) and broodnest size.

plained variation in flight activity better than simple air temperature alone did.

A quadratic relationship also was evident between flight and time of day. When temperature and colony size were held constant, bees flew less actively at later times of the day, but this effect was less pronounced at later times (Fig. 4). The decrease in flight through the day was greater for large colonies than for small colonies.

Pollen foraging rates did not differ between Russian and Italian bees on any of the 4 d of observation (Table 2). Observations of pollen loads when handling bees indicated only almond pollen was being collected.

The predicted flight activity was not directly influenced by the effect of bee type when all environmental effects were accounted for. However, the observed flight from Russian colonies overall was 71% of that from Italian colonies (Fig. 5). This difference largely occurred because of the relatively smaller populations of Russian colonies, which on average had 76% of the adult bees and 78% of the brood of Italian colonies (Table 3; Fig. 6). Given this difference in colony sizes, we produced a reduced data set of equal-sized colonies and conducted another ANOVA to verify a lack of any effect of bee type. The reduced data were obtained by eliminating the largest nine Italian colonies and the smallest nine Russian colonies (based on adult bee populations); the resulting mean colony sizes were 6.71 frames of bees in Italian colonies and 6.74 frames of bees in Russian colonies. The analysis using these data again showed no significant influence of bee type on flight activity ( $F = 0.12$ ;  $df = 1,588$ ;  $P = 0.732$ ). The predicted flight activity across the range of

Table 2. Percentages (mean  $\pm$  SE) of returning foragers of the two bee types that carried pollen during almond pollination in 2002

Bee type	26 Feb.	27 Feb.	3 Mar.	4 Mar.
Italian	64.6 $\pm$ 2.5	49.8 $\pm$ 2.9	18.6 $\pm$ 2.6	19.7 $\pm$ 2.1
Russian	64.1 $\pm$ 2.5	46.8 $\pm$ 2.3	16.5 $\pm$ 2.3	17.1 $\pm$ 1.7

Samples were from 19 Italian and 23 Russian colonies. There were no differences between the bee types on any of the four sampling dates ( $P \geq 0.34\text{--}0.89$ ;  $t$ -tests).

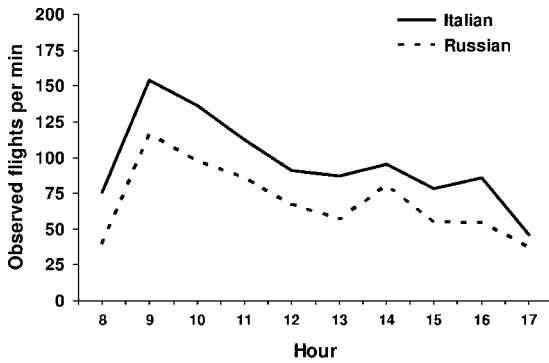


Fig. 5. Observed hourly flight activity of Italian and Russian bees during almond pollination. Results are means from 9 d of counts.

reduced data was congruent with the flight predicted from the full data set (Figs. 1 and 2).

**Discussion**

The positive association of honey bee flight activity with colony size and temperature was expected based on previous research. Gary et al. (1978) measured adult bee population and foraging during almond bloom and found a linear increase in foraging activity from larger colonies. Our similar finding supports their earlier conclusion that larger colonies are proportionally, not disproportionately, more valuable as pollinators than smaller colonies. For a colony of average size (6.82 frames of bees and 1,484-cm<sup>2</sup> brood), flight activity increased by almost 10% with an additional frame entirely covered with bees and by 40% with an additional full frame of brood. Note that Edson (1977) reported greater differences in flight between large and small colonies under cooler conditions. Weather during our test in 2002 was unusually warm, with an average daily maximum temperature of 23.3°C (74°F) (range, 19.5–27.3°C [67–81°F]).

Temperature plays a key role when flight is not limited by precipitation, light, or wind (Lundie 1925; for review, see Kevan and Baker 1983). A decrease in the influence of temperature later in the day (a quadratic relationship) has not been reported previously (e.g., Burrill and Dietz (1981) suggested an approximately linear relationship). It is consistent, however, with the observation that honey bee flight often ceases

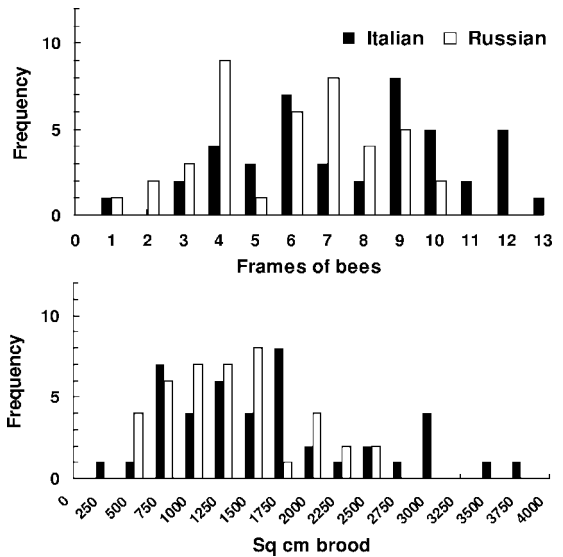


Fig. 6. Distribution of colony sizes of Italian and Russian bees.

at the end of the day at temperatures higher than those at which flight is initiated (Burrill and Dietz 1981). Furthermore, the trend of diminished flight at later times of day (even when temperatures are suitable for foraging) may be a consequence of diminished nectar and pollen availability in the field rather than a primary effect of time.

The minimum temperature threshold for flight predicted here (12–13°C, ≈54–55°F) is within the range of black globe values (7.4–13.4°C, ≈45–56°F) reported by Corbet et al. (1993) from observations of bees foraging under different resource conditions. The better predictiveness of black globe temperatures than that of ambient air temperatures also is consistent with the findings of Corbet et al. (1993). These two studies are the only studies to report black globe data for honey bees. Generally, however, the temperature effects we found are in agreement with other reports involving air temperatures (Lundie 1925, Burrill and Dietz 1981, Vicens and Bosch 2000).

The late-winter bee populations were smaller in Russian than in Italian colonies. Although unrecognized environmental differences at the two overwintering sites could have attributed to this result, we have seen a similar trend of smaller bee populations in Russian colonies in other experiments and beekeeping situations (unpublished observations). Smaller populations resulted in less foraging activity. Beekeepers may want to compensate for this by stimulating colony growth by feeding pollen, pollen substitutes or carbohydrates before using Russian colonies for early pollination service. Russian and Italian colonies of the same size are likely to be similarly effective pollinators, because these bee types did not differ in the major colony-level, pollination-related traits we measured (flight activity and proportion of pollen foragers). Comparative measurements of for-

Table 3. Colony sizes (mean ± SE) of the two bee types and results of *t*-tests comparing the types within each size category

Bee type	Frames of adult bees	Sealed brood (cm <sup>2</sup> )
Italian ( <i>n</i> = 43)	7.70 ± 0.44	1,658 ± 131
Russian ( <i>n</i> = 41)	5.89 ± 0.36	1,297 ± 88
	<i>t</i> = 3.18, <i>df</i> = 82, <i>P</i> = 0.002	<i>t</i> = 2.29, <i>df</i> = 72.7 <sup>a</sup> , <i>P</i> = 0.025

Adult bee numbers are frames of bees. Brood is the sq cm of sealed brood.

<sup>a</sup> *df* adjusted by Satterthwaite method because of unequal variances.

aging traits of individual bees, and especially of direct pollination effectiveness, would be useful to more fully assess this projection. Finally, we found no evidence to support anecdotal accounts of Russian colonies having more flight activity in cool conditions and engaging in greater pollen foraging.

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