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Original article

Quantification of cluster size and low ambient temperature relationships in the honey bee

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Summary — Cluster volume and surface area were measured over a range of ambient temperatures (T_a) in 3 honey bee colonies representative of small, medium and large populations from 29 November 1984 to 21 March 1985. Changes in these parameters were correlated with changes in T_a, and the observed response to T_a was independent of population size. We observed decreases of about 55% in cluster volume and 40% in cluster surface area as the T_a decreased from 4 °C to –23 °C.

***Apis mellifera* / cluster size / homeothermy / honey consumption / thermoregulation**

INTRODUCTION

Although the honey bee (*Apis mellifera* L) probably originated in the African or Asian tropics (Ruttner, 1988), present-day descendants living in Europe and other temperate regions have evolved adaptations for thermoregulation which enable successful colonization and survival in extremely cold climates. Survival in cold winter climates is primarily due to their system of food storage and clustering into a tight mass thereby reducing heat loss. Adaptation to cold climates does not involve a state of dormancy or hibernation characteristic of most insects; honey bees remain active within the winter cluster. The cluster center, or core, in broodless colonies is generally maintained within the range of 20–30 °C (Gates, 1914; Wilson and Milum, 1927; Corkins, 1930; Owens, 1971, Szabo, 1985, 1989). During brood rearing, core temperatures range from 29–36 °C (Owens, 1971; Szabo, 1985). The cluster periphery remains relatively isothermal at *ca* 9 °C (Owens, 1971; Southwick, 1988).

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Research, relative to low ambient temperature (T_a) survival, has generally concentrated on the role of metabolism (*i e,* honey consumption for heat production) in colony-level thermoregulation. Evidence suggests that increased levels of metabolism are indeed associated with exposure to cold temperatures. Free and Simpson (1963) reported that cluster CO_2 production is minimal at about 10 °C and increases above or below this temperature. Measurements of cluster O_2 consumption support these results (Southwick and Mugaas, 1971; Southwick, 1982, 1983, 1985a, 1985b, 1988).

Individual bees (Free and Spencer-Booth, 1960) and small groups of bees (Cayhill and Lustick, 1976) are unable to efficiently thermoregulate when subjected to cold temperatures and soon perish. However, an intact cluster within a nest can, effectively thermoregulate, and has been likened to a homeothermic superorganism (Southwick, 1983). It has been suggested that temperature-mediated alterations of cluster dimensions may maximize conservation of heat produced by bees within the cluster (Corkins, 1932; Simpson, 1961; Heinrich, 1981; Severson and Erickson, 1985). However, it has also been suggested that no precise relationship exists between cluster expansion and contraction with the T_a, and that the limits of cluster contraction are reached at about 0–5 °C (Seeley and Heinrich, 1981; Southwick, 1988). However, this hypothesis is, based on cursory observations of cluster activity (Gates, 1914; Owens, 1971; Szabo, 1985). In this study, we provide the first quantitative evidence for a relationship between changes in cluster volume and surface area and T_a in honey bee colonies.

MATERIALS AND METHODS

Data collection

This study was conducted at Madison, WI, USA from 29 November 1984 to 21 March 1985. Three honey bee colonies (Italian-type), representative of small (SP), medium (MP) and large (LP) populations were selected for periodic monitoring of cluster volume and surface area. Estimates of population sizes in November were 18, 40, and 65 thousand bees, respectively. These estimates were based on comparisons of test colony volume measurements at 4 °C to those observed among colonies in a related study, in which the entire worker bee population was collected and counted following volume measurement (Severson and Erickson, unpublished data). All colonies consisted of 12-comb, 16.5 cm-deep, square (50.5 cm) hive-bodies; the SP and MP colonies were maintained in 3 hive-bodies, while the LP colony was maintained in 4 hive-bodies. Individual colony lower entrances were closed and an upper entrance (2.54 cm auger hole) provided.

The first data were collected on 29 November 1984; the T_a was sufficiently low (4 °C), so the clusters were well-defined at this time. The T_a was always recorded at the apiary site (*e g,* at a single point within about 2 m from the individual colony locations) immediately prior to cluster measurements. Initial data collection involved separating the hive-bodies of each colony, and when the cluster extended from top to bottom of a hive-body, measuring cluster diameters at the top and bottom of each. Cluster depth in the topmost and lowest occupied hive-body was also measured. Thereafter, these measurements were gathered from intact colonies using a Volpi type 51500 intrascope (a fiber optics wand) equipped with a red filter. The use of this unit under red light conditions allowed visual determination of cluster location with minimal cluster perturbation. To facilitate data collection with this unit, 2 rows of 0.9 cm holes were drilled through the hive-bodies (from and back) between each comb:

— up 1.5 cm from the bottom of each hive-body; and

— along the center of each hive-body. The holes were then plugged with corks. During data collection, individual corks were removed and the fiber optics wand inserted to the edge of the cluster, and the minimum insertion length was recorded (*e g,* the minimum distance between the cluster and the hive wall). Such measurements from the front and back of a colony allowed determination of cluster diameter (length). Diameter from side-to-side (width) was measured by examining comb interspaces and determining how close to each side the cluster extended. When a cluster did not extend from top to bottom of a hive-body (as was occasionally observed in the topmost and lowest occupied hive-bodies), the cluster depth within that hive-body was recorded. These measurements generally defined a series of ellipses which were used to calculate cluster volume and surface area (fig 1).

Data analyses

Statistical analyses were made using the Statistical Analyses System (SAS) for computer data analyses. Percent reduction values for volume and surface area were determined by comparing an observation at a given T_a to the respective initial observation on 29 November 1984 (4 °C). However, the data were influenced by the extreme cold weather which occurred between 20 January (d 69) and 2 February 1985 (d 82) (fig 2). The observed cluster response to temperature suggested that sufficient mortality levels had occurred to reduce colony population sizes during this period. Since the response to temperature was based on the original population size, percent reduction values observed after d 82 (post-cold weather) remained consistently higher than those collected before d 69 (pre-cold weather). Therefore, data collected between days 69 and 82 were not utilized in modeling cluster response to T_a. Furthermore, extensive population loss was observed in the SP colony on 18 February due to starvation; data collected from this colony after this date were also not utilized in the development of empirical models.

A nonlinear (NLIN) procedure was used to develop empirical models for the observed relationships between the T_a and :

— percent volume reduction; and
— percent surface area reduction.

$V = \Sigma V_H$, where;

$V_H = \frac{\pi h}{6}(2ab + aB + Ab + 2AB)$

$S = \Sigma S_E + \Sigma S_F$, where;

$S_E = \pi AB$;

$S_F = \pi(\bar{r}_1 + \bar{r}_2)\sqrt{h^2 + (\bar{r}_1 - \bar{r}_2)^2}$, where;

$\bar{r}_1 = \frac{A+B}{2}$ and $\bar{r}_2 = \frac{a+b}{2}$

A and B = respective radii of the upper ellipse
a and b = respective radii of the lower ellipse
h = distance between upper and lower ellipses

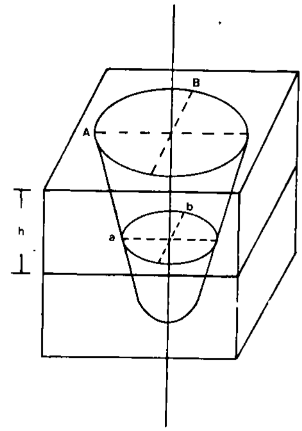

Fig 1. Equations for calculating cluster volume *(V)* and surface area *(S)*. The equation for *V* is taken from Severson and Erickson (1984). V_H = the cluster volume in 1 hive-body. S_E is the standard equation for measuring the surface area of an ellipse; it was used to determine the surface areas of the cluster top and bottom whenever these surfaces were relatively flat. S_F is a modification of the equation for determining the area of the curved surface of a frustum of a right cone (Selby and Girling, 1965); it was used to estimate the surface area of the cluster perimeter in each hive-body.

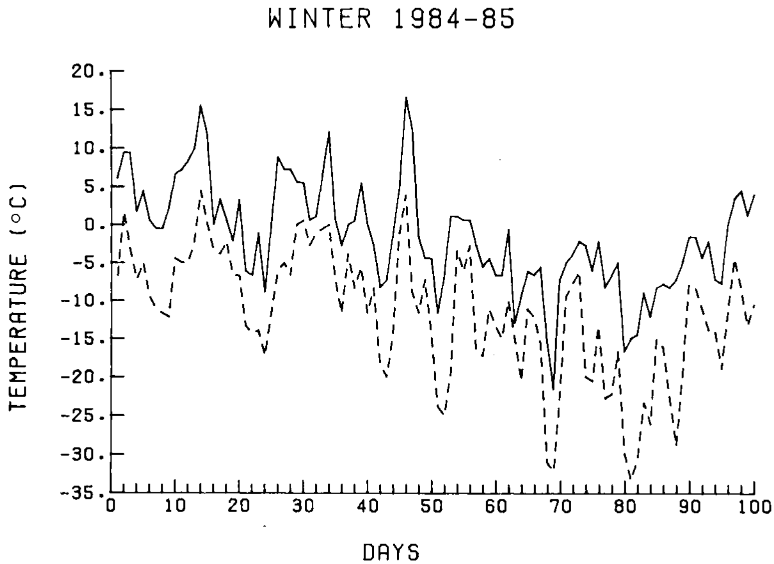

Fig 2. Maximum (solid line) and minimum (broken line) temperatures observed from 12 November 1984 (d 0) to 18 February 1985 (d 98).

To account for the observed reduction in population sizes between days 69 and 82, an indicator or dummy variable (Severson *et al*, 1987, for an in-depth explanation on the use of indicator variables) was included in the analyses. Briefly, the use of an indicator variable allowed us to fit our data to equations where the intercept values depended upon the period of sample collection (pre-cold *versus* post-cold).

RESULTS

Exponential models, representing the best fit (least squares criterion) to the observed data sets, were derived to describe cluster response to T_a in terms of percent:

— volume reduction; and

— surface area reduction.

Cluster percent volume reduction *(V)* increased as T_a decreased, following the equation: $V = 58.16\ (1 - e^{-0.118\ (4-Ta)}) + 15.77\ (I)$ (table I). Cluster percent surface area reduction *(S)* increased as T_a decreased, following the equation: $S = 44.44\ (1 - e^{-0.86(4-T_a)}) + 11.33\ (I)$ (table II). The indicator variable *(I)* was set equal to 1 for data collected after d 82 otherwise $I = 0$. Cluster response to T_a was independent of colony size although the 3 colonies represented extremes in population size, the observed responses to T_a were identical. An ability to reduce volume and surface area reduction values was clearly evident to at least –23 °C. The use of an indicator variable *(I)*, to account for the observed cold-weather decrease in population sizes, demonstrated that cluster response to T_a was the same before 19 January (pre-cold weather) and after 4 February (post-cold weather).

DISCUSSION

Our results indicate that the honey bee winter cluster expands and contracts in a

Table I. Cluster volume (cm3) and volume reduction (%) relative to ambient temperature (Ta).
[a] Percent reduction was arbitrarily set at zero relative to the initial measurements at 4 °C; [b] Pre-cold weather data were collected from 29 November 1984 to 19 January 1985. [c] Post-cold weather data were collected from 4 February to 26 March 1985. [d] No data. [e] Data not included as SP colony experienced extensive population loss due to starvation on 18 February.

Date	T_a	*SP*		*MP*		*LP*	
		cm^3	%	*cm*^{3}	%	*cm*^{3}	%
Pre-cold: [b]							
9 November 1984	4	12 800	0 [a]	29 859	0 [a]	49 492	0 [a]
10 January 1985	–5	7 163	44.00	– [d]	–	–	–
11 January 1985	–8	7 074	44.73	–	–	–	–
14 January 1985	–6	7 644	40.28	–	–	28 671	42.07
15 January 1985	–15.5	6 236	51.28	–	–	25 530	48.42
16 January 1985	–9	7 301	42.96	16 038	46.29	26 969	45.51
18 January 1985	–8	7 162	44.05	16 452	44.90	25 592	48.29
19 January 1985	–23	5 343	58.26	11 260	62.29	21 979	55.59
Post-cold: [c]							
4 February 1985	–19	3 413	73.34	8 775	70.61	17 230	65.19
6 February 1985	–12	4 708	63.22	12 145	59.33	16 702	66.25
19 February 1985	–6.5	+ [e]	+	14 030	53.01	22 265	55.01
20 February 1985	–2.25	+	+	15 626	47.67	27 593	44.25
22 February 1985	2.5	+	+	19 694	34.04	29 948	39.49
25 February 1985	–0.75	+	+	17 862	40.18	36 043	27.17
26 February 1985	–2.25	+	+	18 196	39.06	37 394	24.44
21 March 1985	3.25	+	+	22 670	24.08	43 485	12.14

predictable manner relative to changes in the T_a. This suggests that individual clusters are able to efficiently regulate heat loss from the cluster surface. In addition, cluster volume and surface area continue to decrease as the T_a decreases to at least – 23 °C. We observed decreases of about 55% in cluster volume and 40% in cluster surface area as the T_a decreased from 4 °C to – 23°C.

The observed response of individual clusters to changes in ambient temperature was independent of colony population size. We observed identical changes in relative surface area and volume in clusters consisting of *ca* 18, 40, and 65 thousand bees. This phenomenon would, however, promote differential heat loss relative to population size. As the number of individual bees within the cluster increases, proportionally fewer bees are exposed to T_a. An equal rate of heat loss per unit of colony population size would only be possible if colonies with smaller populations exhibited greater reductions in cluster size as the T_a decreased. Colonies with large populations do, therefore, exhibit a greater ability to maintain cluster core temperature (Free and Spencer-Booth, 1958; Southwick, 1985b, 1987). Moreover, since an object with a small surface area to volume ratio *(SV)* loses heat at a lower rate than one with a large *SV*, one would expect a large colony (small *SV)* to be able to maintain

Table II. Cluster surface area (cm^2) and surface area reduction (%) relative to ambient temperature (T_a). See Table I for descriptions.

		SP		MP		LP	
Date	T_a	cm^2	%	cm^2	%	cm^2	%
Pre-cold: [b]							
9 November 1984	4	2 834	0	5 130	0	6 922	0
10 January 1985	–5	1 901	32.92	–	–	–	–
11 January 1985	–8	2 123	25.09	–	–	–	–
14 January 1985	–6	2 125	22.55	–	–	4 855	29.86
15 January 1985	–15.5	1 961	30.80	–	–	4 610	33.40
16 January 1985	– 9	2 163	23.68	3 582	30.18	4 707	32.00
18 January 1985	–8	2 102	25.83	3 519	31.40	4 481	35.26
19 January 1985	–23	1 829	35.46	2 732	46.74	4 178	39.64
Post-cold: [c]							
4 February 1985	–19	1 419	49.93	2 439	52.46	3 643	47.37
6 February 1985	–12	1 669	41.11	2 949	42.51	3 490	49.58
19 February 1985	–6.5	+	+	3 157	38.46	4 119	40.49
20 February 1985	–2.25	+	+	3 332	35.05	4 727	31.71
22 February 1985	2.5	+	+	4 045	21.15	5 001	27.75
25 February 1985	–0.75	+	+	3 734	27.21	5 729	17.23
26 February 1985	–2.25	+	+	3 726	27.37	5 869	13.77
21 March 1985	3.25	+	+	4 222	17.70	6 351	8.25

high cluster temperatures with a lower metabolic expenditure than would a small colony (large *SV*). This hypothesis is supported by measurements of colony honey consumption rates: average honey consumption rate per unit of colony size decreases as colony size increases (Free and Racey, 1968; Harbo, 1983; Severson and Erickson, unpublished data).

Permanent reductions in cluster size, indicative of a loss in total population, were observed in each colony following exposure to T_a of – 30 °C or less (during the period between 19 January and 4 February). Individual colonies comprised of at least 13 000 – 15 000 bees can, however, survive exposure to T_a of –80 °C for short periods (Southwick, 1987). Colony survival during periods of exposure to T_a below about –23 °C may, therefore, depend largely upon increased heat production.

Since bees within the cluster would not perceive changes in T_a before those at the cluster periphery had entered chill-coma, it is likely that the peripheral bees are largely responsible for maintaining cluster homeothermy. Perception of changes in T_a and the corresponding alteration of cluster parameters by peripheral bees provides a mechanism for conservation of heat produced by bees within the cluster (Heinrich, 1981).

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Résumé — Quantification des relations entre la taille de la grappe d'abeilles et les basses températures ambiantes. Le volume et la surface de la grappe d'abeilles ont été mesurés à diverses températures ambiantes *(T_a)* dans 3 colonies représentant des populations de petite (SP), moyenne (MP) et grande (LP) taille, du 29 novembre 1984 au 21 mars 1985 à Madison, Wisconsin (USA). Pour calculer le volume et la surface de la grappe, on a mesuré son diamètre et sa profondeur à l'intérieur des corps de ruche (fig 1). Les valeurs ont été comparées à celles de la T_a. Des modèles exponentiels, représentant la meilleure adaptation aux données recueillies, ont été développés pour décrire la réponse de la grappe à la T_a. Les variations observées dans le taux de réduction du volume (tableau I) et de la surface (tableau II) en fonction de la T_a sont indépendantes de la taille de la population. Les taux de réduction du volume *(V)* et de la surface *(S)* de la grappe augmentent quand la T_a décroît, selon les équations: $V = 58{,}16\ (1 - e^{-0{,}118(4-T_a)}) + 15{,}77$ *(l)* et $S = 44{,}44\ (1 - e^{-0{,}86(4-T_a)}) + 11{,}33$ *(l)*. Nous avons observé une diminution d'environ 55% du volume et 40% de la surface de la grappe lorsque la température est passée de 4 °C à – 23 °C.

***Apis mellifica* / homéothermie / grappe hivernale / consommation de miel / thermorégulation**

Zusammenfassung — Quantifizierung der Beziehungen zwischen der Größe der Wintertraube und niedriger Außentemperatur bei der Honigbiene. Volumen und Oberfläche der Bienentraube wurden bei den auftretenden Außen- temperaturen *(T_a)* zwischen 29. November 1984 und 21. März 1985 in Madison, WI, USA, bei drei Bienenvölkern gemessen, die nach ihrer Stärke als schwach, mittel und stark gelten konnten. Um Volumen und Oberfläche zu berechnen, wurden Durchmesser und Tiefe der Traube in den Kästen gemessen (Abb 1). Die Werte wurden anschließend mit der T_a verglichen. Es wurden exponentielle Modelle mit der besten Anpassung an die beobachteten Daten abgeleitet, um die Reaktion der Traube auf die T_a zu beschreiben. Die beobachteten Verände- rungen in der prozentuellen Verringerung von Volumen und Oberfläche in Bezug auf die T_a waren unabhängig von der Volksstärke. Die prozentuelle Reduktion des Volumens der Traube (V) stieg mit fallender T_a nach folgender Gleichung an: $V = 58{,}16\ (1 - e^{-0{,}118\ (4-T_a)}) + 15{,}77$ *(l)*. Die prozentuelle Reduktion der Trauben- oberfläche *(S)* nahm nach folgender Gleichung mit abnehmender T_a zu: $S = 44{,}44\ (1 - e^{-0{,}86(4-T_a)}) + 11{,}33$ *(l)*. Wir beobachteten Abnahmen des Trauben- volumens um etwa 55% und der Traubenoberfläche um 40% wenn die T_a von 4 °C auf – 23 °C absank.

***Apis mellifera* / Homeothermie / Wintertraube / Honigkonsum / Temperatur-Regulierung**

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