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Body size and reproductive success of drones (*Apis mellifera* L)

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Summary — We compared drones of different body size. Small drones were reared in worker cells while large drones originated from drone cells. We used the cordovan (cd) mutant as a marker. The distribution of drone types in a drone congregation area was monitored by pheromone traps. No significant differences in temporal, horizontal and vertical distributions of large (cd) drones were found, either in comparison with large (+) or in the experiment with small (+) drones. The offspring of homozygous cordovan (cd/cd) queens which were mated during the experiment by (cd) and (+) drones was examined. We compared the ratio of (cd/cd) and (cd/+) workers to the drone ratio at time of the mating flight. Small drones had a reproductive disadvantage compared with large drones. Large (cd) drones had a lower reproductive success compared to large (+) drones.

***Apis mellifera* / drone / body size / reproductive success / offspring analysis**

INTRODUCTION

For some Apoidea (*Chilalictus* and *Lasioglossum* species) different morphs of males are described which are linked to different behaviors (Rayment, 1955; Houston, 1970; Kukuk and Schwarz, 1988). For the ant *Formica exsecta* and the wasp *Polistes dominulus* body size dimorphism of drones is not associated with different social tasks. As a rule, males of social Hymenoptera do not play a major role in the division of labor. The different males, however, follow alternative mating strategies (Fortelius et al, 1987; Beani and Turillazzi, 1988).

For production of drones, *Apis mellifera* queens lay unfertilized eggs in larger comb cells ('drone cells') (Koeniger, 1970). In the case of depletion of the queen's sperm stor-

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age or for several other reasons, a few unfertilized eggs are commonly found in the smaller worker cells. These eggs are reared and result in drones which are significantly smaller than the drones that emerge from drone cells (Gontarski, 1938; Berg, 1991).

Mating in *Apis mellifera* takes place in a drone congregation area high in the air (Jean-Prost, 1957; Koeniger et al, 1979). There, the flying young queen is regularly followed by large swarms of drones which compete for mating (Gries and Koeniger, 1996). It is not known yet whether small drones follow a mating strategy which is different from the strategy of large drones. In this paper we present data on the distribution of both drone types within the drone congregation area. Further, we compare the reproductive success of large and small drones.

MATERIALS AND METHODS

The experiments were carried out with drones and queens of *Apis mellifera carnica*. The studies were conducted from 1989 and 1990 in the region of Wildalpen (Steiermark, Austria) in a drone congregation area situated in a valley 600 m above sea level. This drone congregation area is surrounded by mountains ranging from 1 800 to 2 300 m above sea level. A few local bee colonies were fitted with drone excluders at the hive entrances, preventing drone flight from any colonies not in the experiment. During a 2-week period the drone composition was adjusted according to our experimental needs by placing drone colonies in the valley. These contained either small drones originating from worker cells or large drones reared in drone cells. The drones were genetically marked using the recessive cordovan mutant, ie, (cd) drones had a light body color while (+) drones were dark (table I).

Ten colonies of each type of drone were placed in the valley side by side. All hive entrances were provided with removable drone excluders. In the drone congregation areas, drones were caught by drone traps lifted by balloons (Taylor, 1984; Williams, 1987). The captured drones were counted, classified on the spot as dark (+) or light (cd), and released. The time of confinement in the drone trap was kept shorter than 10 min. Drones were consistently caught in the center of the drone congregation area (fig 1, III). In 1989 drones were also caught in different locations within the drone congregation area. Five permanent trapping stations were installed at distances of 50 m (fig 1, I–V). Drones were caught between 15 and 25 m above ground. When large drones were flying we only caught drones in locations III–V. Drone catches at different heights were carried out in the center of a DCA in a valley near Kronberg in Germany.

Virgin queens (n = 40–50 per week) were introduced into small colonies within 1 km of the drone congregation area. All queens were homozygous cordovan (cd/cd). At the hive entrances glass tubes with queen excluders were installed for observations of queen flights. Queens could not pass the excluder and had to be set free for flight. Returning queens were carefully inspected for signs of mating. Times of start and return were recorded (Koeniger et al, 1989).

Between 15 and 20 days after the start of oviposition of the mated queens, combs with sealed brood were taken and placed in separate cages in an incubator (34.5 °C, 70% relative humidity). The emerged bees were collected daily and classified according to their body color (table II).

For size confirmation of the two drone groups, the right forewing was removed and measured according to Ruttner et al (1978). In this way drone samples previously classified according to their body color in the field were compared to control groups of drones which had emerged from worker or drone cells in an incubator (table III).

Table I. Drone compositions.

	1 type	*2 type*
Week 1	large (cd) drone	large (+) drone
Week 2	large (cd) drone	small (+) drone

(cd): cordovan = light; (+): wild type = dark.

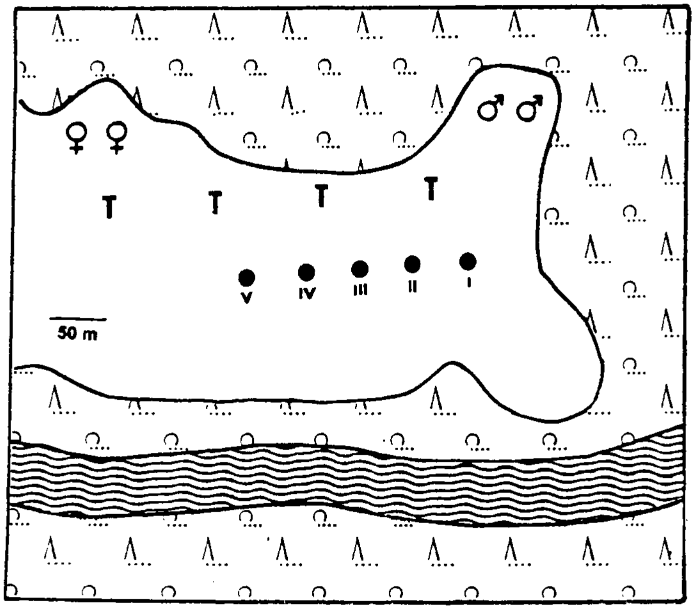

Fig 1. Map of drone congregation area. I–V: permanent stations for drone catches (for the horizontal distribution); III: central location of DCA. ♀♀: virgin queens; ♂♂: drone colonies; T: pylon; [river symbol]: river; [forest symbol]: forest.

Table II. Phenotype and parent analysis of the young worker bees.

Phenotype (body color) of worker bee	*Genotype worker*	*Genotype mother*	*Genotype father*
Dark	(+/cd)	(cd/cd)	(+)
Light	(cd/cd)	(cd/cd)	(cd)

(cd): cordovan = light; (+): wild type = dark.

Table III. Comparison of winglength between small and large drones caught on the drone congregation area and drones emerged from worker or drone cells in an incubator.

	Small drone (mm)	*Large drone (mm)*	*t-Test*
Drones from DCA	11.29 ± 0.39 $n = 103$	12.14 ± 0.20 $n = 99$	$P < 0.0001$
Drones from incubator	11.25 ± 0.31 $n = 300$	12.09 ± 0.24 $n = 300$	$P < 0.0001$
t-Test	$P > 0.2$	$P > 0.1$	

RESULTS

Classification of drone type

There was no significant difference in wing length between small drones from the drone congregation area and small drones emerged from worker cells ($P > 0.2$, t-test), or respectively between large drones from drone congregation areas and from drone cells ($P > 0.1$, t-test). The difference in wing length between small and large drones was highly significant ($P < 0.0001$, t-test).

Horizontal distribution of drones in the drone congregation area

On 27 July 1989 we found no significant differences in the composition of large (cd) drones and large (+) drones ($P > 0.1$, $k \times 2$ contingency test) between the trapping stations III, IV and V. In the second week, investigating large and small drones, drones were caught on 3 days (30 July, 4 and 5 August) at different places (table IV). Composition of large and small drones differed between trappings, as well as between trapping stations ($P < 0.0005$, $k \times 2$ contingency tests). Differences in the ratios, however, were not significant between days and places (ANOVA, $P > 0.5$), nor did they show any relation to the distance from the colony (linear regression $y = 7.3 * 10^{-6} * x + 3.78$, $P > 0.99$). This indicated an even distribution of large drones (IV).

Vertical distribution of drones in the drone congregation area.

Drones were caught at different heights ranging between 5 and 35 m. The results of 54 catches, summed for 5-m height intervals, are given in table V. There was no significant difference in the drone composition in relation to catches ($P > 0.23$, $k \times 2$ contingency test) or height intervals ($P > 0.23$ and $P > 0.29$, respectively, $k \times 2$ contingency test), and no relation of the ratio of small to large drones in the 54 catches to the height (linear regression $y = 3.45 * 10^{-4} * x + 9.4$, $P > 0.81$).

Temporal distribution of drone flights

In 1990, drones were caught continuously around the locations III and IV of the DCA, during hours of flight activity (table VI). The proportion of the two drone groups did not differ between the first period (before 1530 hours) and the second period after 1530 hours ($P > 0.1$, 2×2 contingency test).

Table IV. Horizontal distribution of drones.

No (distance to drone colonies)	*n drones, week 1 large (cd) / large (+)*	*Ratio*	*n drones, week 2 large (cd) / small (+)*	*Ratio*
0 (50 m)			106/612*	0.17
I (120 m)	—	—	263/481*	0.53
II (147 m)	—	—	45/99*	0.44
III (173 m)	133/470*	0.28	414/1178***	0.35
IV (213 m)	98/393*	0.25	198/538*	0.37
V (260 m)	125/486*	0.26	166/932**	0.25

cd: cordovan; +: wild type.
* Total of 1 day; ** total of 2 days; *** total of 3 days.

Table V. Vertical distribution of drones in a DCA.

Height (m)	*Catches (n)*	*Small drones*	*Large drones*	*Ratio*
10	21	34	395	0.0860
15	14	127	1125	0.1128
20	7	47	436	0.1077
25	7	41	437	0.0938
30	2	22	320	0.0687
35	3	23	195	0.1179

Table VI. Timetable of drone catches.

	Week 1: n drones large (cd) / large (+)			*Week 2: n drones large (cd) / small (+)*				
Date	20.07	21.07	22.07	23.07	24.07	25.07	26.07	27.07
Hours								
–1330	—/—	—/—	1/23	—/—	0/5	—/—	—/—	—/—
–1400	11/5	5/11	14/213	4/15	—/—	—/—	4/5	6/11
–1430	7/1	6/3	59/374	38/108	5/9	2/5	16/56	2/5
–1500	8/1	7/6	20/88	52/142	8/16	3/6	13/39	3/4
–1530	17/17	8/9	42/82	62/103	1/15	22/37	17/40	25/41
–1600	9/11	2/6	10/40	53/68	13/47	14/30	23/33	7/16
–1630	5/6	3/6	11/62	88/303	17/28	6/14	4/1	5/10
–1700	3/6	2/2	3/59	116/226	4/10	10/18	3/0	12/22
–1730	—/—	2/1	—/—	11/31	5/1	0/1	—/—	20/32
–1800	—/—	—/—	—/—	—/—	5/6	—/—	—/—	—/—

cd: cordovan; +: wild type.

Reproductive success

Samples of the drone population were caught in the area with the highest drone concentration within the drone congregation area (station III) for estimating the probability that a queen would encounter the respective drone type. The mating ratio was calculated by offspring analysis of the queen's daughters (scheme of study technique: fig 2). Assuming that each drone type had an equal reproductive efficiency we would expect a good correspondence between the ratio of the (cd/cd) and (cd/+) worker offspring for each queen and the drone ratio during the day of mating. Significant differences between the ratio of worker types and the drone proportion would indicate differences in the reproductive success of the drone types. The differ-

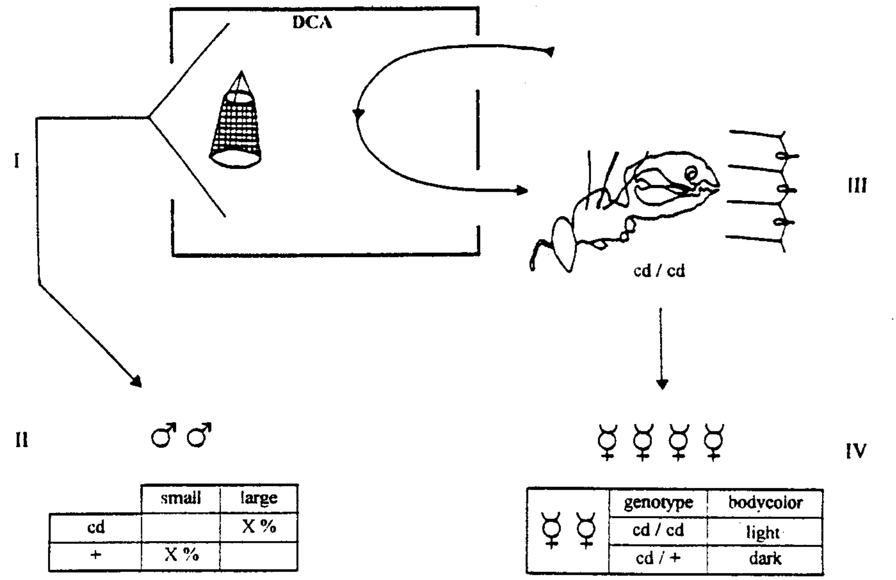

Fig 2. Scheme of study technique to determine drone composition on the DCA and offspring analysis. cd: cordovan; DCA: drone congregation area; +: wildtype; I: drone catches on DCA; II: determination of drone composition; III: mating of queens on DCA; IV: offspring analysis.

ences between the percentage of the (cd/cd) worker offspring and the (cd) drones during the mating day were listed for each queen (table VII). A positive difference indicates a higher reproductive success of (cd) drones. A negative difference indicates a lower (cd/cd) percentage in the offspring and a higher ratio of (cd) drones in the drone congregation area, which means a lower reproductive success.

In the first weeks of 1989 and 1990 we had large (cd) drones versus large (+) drones. In both years more negative (n = 30) than positive (n = 16) differences could be found (table VII a,c; $P < 0.05$, sign-test Dixon and Mood). Therefore, when both groups consisted of large drones there was a reproductive disadvantage of cd drones. In 1990, these differences were significant ($P < 0.01$, sign-test Dixon and Mood). In 1989, with only 1 day of favorable weather conditions for mating flights, the results showed the same tendency, but were not significant.

In the second week we had large (cd) drones versus small (+) drones (table VII b,d). More positive than negative (30 and 17, respectively) differences were found indicating a reproductive advantage of the large (cd) drones ($P < 0{,}05$, sign-test Dixon and Mood). Those differences were significant in 1990 ($P < 0.01$, sign-test Dixon and Mood). They were not significant but displayed the same trend in 1989, when all mating flights besides one (4.8.) occurred on the 5 August (table VII b).

DISCUSSION

These experiments demonstrate the reproductive disadvantage of small drones. When both drone groups were of the same size

Table VII a, b. Comparison of (cd) offspring ratio and (cd) drone ratio in the DCA during the day of the queen's mating (1989).

a, Week 1: large (cd) drones versus large (+) drones.

Queen	*n worker*	*% cd workers*	*% cd drone*	*Difference %*
a, Week 1: large (cd) drones versus large (+) drones.				
365	430	72.1	24.8	+47.3
447	351	65.8	24.8	+41.0
371	550	58.6	24.8	+33.8
523	746	48.4	24.8	+23.6
397	557	42.2	24.8	+17.4
398	367	40.1	24.8	+15.3
509	358	37.2	24.8	+12.4
453	635	31.2	24.8	+ 6.4
400	499	29.1	24.8	+4.2
373	414	24.2	24.8	–0.6
369	557	12.4	24.8	–12.4
377	450	6.0	24.8	–18.8
512	296	4.1	24.8	–20.7
372	496	2.8	24.8	–22.0
367	730	2.2	24.8	–22.6
362	672	1.8	24.8	–23.0
379	449	0	24.8	–24.3
386	503	0	24.8	–24.8
392	365	0	24.8	–24.8
b, Week 2: large (cd) drones versus small (+) drones.				
326	382	100.0	11.3	+88.7
364	376	64.4	11.3	+53.1
330-	514	52.9	11.3	+41.6
381	266	42.9	11.3	+31.6
237	280	45.4	15.5	+29.9
098	345	24.6	11.3	+13.3
343	392	24.5	11.3	+13.2
356	309	22.7	11.3	+11.4
006	133	17.3	11.3	+6.0
010	125	16.8	11.3	+5.5
310	357	14.6	11.3	+3.3
360	316	14.2	11.3	+2.9
370	496	9.3	11.3	–2.0
323	285	9.1	11.3	–2.2
384	638	7.7	11.3	–3.6
325	450	6.0	11.3	–5.3
319	380	5.8	11.3	–5.5
351	383	0.8	11.3	–10.5
338	259	0	11.3	–11.3
097	264	0	11.3	–11.3
346	304	0	11.3	–11.3
350	230	0	11.3	–11.3

Table VII c, d. Comparison of (cd) offspring ratio and (cd) drone ratio in the DCA during the day of the queen's mating (1989).

c, Week 1: large (cd) drones versus large (+) drones.

Queen	*n worker*	*% cd workers*	*% cd drone*	*Difference %*
c, Week 1: large (cd) drones versus large (+) drones.				
365	430	72.1	24.8	+47.3
271	201	63.7	43.8	+19.9
272	160	26.3	18.2	+8.1
163	225	51.6	43.8	+7.8
264	175	25.7	18.2	+7.5
115	101	100.0	43.8	+6.2
148	110	100.0	67.5	+2.5
224	156	16.0	18.2	−2.2
198	203	35.5	43.8	−8.3
077	153	28.1	18.2	−9.9
184	160	33.1	43.8	−10.7
229	126	6.4	18.2	−11.3
239	229	2.6	18.2	−15.6
154	207	51.2	67.5	−16.3
193	170	23.5	43.8	−20.3
259	223	23.3	43.8	−20.5
017	260	40.0	67.5	−27.5
222	182	37.9	67.5	−29.6
255	152	7.9	43.8	−35.9
245	152	30.9	67.5	−36.6
144	167	30.5	67.5	−37.0
202	126	4.3	43.8	−39.0
032	114	3.5	43.8	−40.3
246	123	1.0	43.8	−42.3
211	119	0	43.8	−43.8
072	234	19.2	67.5	−48.3
200	100	0	67.5	−67.5
d, Week 2: large (cd) drones versus small (+) drones.				
220	106	100.0	31.7	+68.3
187	100	100.0	36.9	+63.1
105	105	100.0	36.9	+63.1
252	108	100.0	36.9	+63.1
042	110	100.0	36.9	+63.1
213	134	94.3	31.7	+62.6
059	161	93.2	36.9	+56.3
104	105	81.0	36.9	+44.1
002	250	71.2	35.1	+36.1
125	202	67.3	36.9	+30.9
134	113	66.1	36.9	+29.2
065	202	60.9	36.9	+24.0
088	118	51.7	36.9	+14.8
052	109	49.5	36.9	+12.6
026	252	36.9	31.7'	+5.2
029	107	43.0	36.9	+6.1
260	233	39.1	36.9	+2.2
108	196	33.7	31.7	+2.0
362	231	33.3	36.9	−3.1
161	184	26.1	36.9	−10.3
152	188	20.2	36.9	−16.7
075	135	12.4	31.7	−19.3
031	145	0.7	36.9	−36.2
182	119	0	36.9	−36.9
101	107	0	36.9	−36.9

(large), the (cd) drones had a reproductive disadvantage compared to the (+) drones. In the second week large (cd) drones had a higher reproductive success than small (+) drones.

In honeybees the brood cell has significant consequences on the development of female larvae. Fertilized eggs in large queen cells are fed differently by the workers and become queens while the female larvae in smaller worker cells are reared to worker bees. However, the small drones (from worker cells) are generally considered as small replicas of the normal (larger) drones (which were reared in bigger drone cells) though a certain amount of physiological difference (as yet unknown) linked to cell-dependent rearing conditions may exist. Nevertheless, differences in body size between both drone types are very obvious and size influences many physiological and behavioral characters. Thus it seems to be appropriate to discuss the difference between the two drone types mainly as differences between small and large drones.

Behavioral interactions among drones during mating flights occur frequently (Koeniger, 1988). Recent experimental studies of flying drones attracted by a fast moving queen dummy revealed a surprising behavioral adaptability of the drone's strategy to different mating situations (Gries and Koeniger, 1996). Competition behavior of males which results in an active displacement of competitors from superior mating territories is quite common in species with male mating assemblies (lekking) and as a result of this the larger males usually occupy territories or locations where the probability of access to the females is optimal (Blum and Blum, 1979; Thornhill and Alcock, 1983; Alcock and Houston, 1987). The distribution of the two drone types in the drone congregation area, however, did not differ significantly.

For comparison with the offspring ratio we considered the proportion of drone types in the drone congregation area. A sampling bias of the trapping technique would result in over or under estimation of the drone-type frequency at the drone congregation area. Such bias, however, is rather unlikely. The queen attracts drones mainly by the means of 9-ODA and drones react to this pheromone over a long distance (Loper et al, 1987; Vallet and Coles, 1993). We applied the same pheromone for baiting our traps. The drones attracted to the baits formed clusters similar to drones which followed free flying queens.

The comparison of the offspring analysis and the drone presence in the drone congregation area showed a reproductive disadvantage of smaller drones. Generally, reasons for a reproductive disadvantage of smaller males can be due to a smaller reproductive potential, eg, amount of sperm, size of spermatophore or the duration of copulation which affects the amount of sperm transferred (Trivers, 1985; Thornhill and Alcock, 1983). For the two drone types in *A mellifera* the number of spermatozoa are not different (Berg, 1990). Further, the duration of copulation in honey bees is independent of the drone because he loses his motility in the moment of everting his endophallus, which inevitably happens at the start of the copulation. Therefore, we hypothesize that the lessened reproductive success of smaller drones is caused mainly by a lower success rate in competition for access to the queen rather than reduced individual inefficiency during the copulatory process.

Altogether the lower reproductive success of small drones fits well with the concept of costs and benefits. Smaller drones should have less reproductive success, which was demonstrated in our experiments. Otherwise drones should be selected for smaller weight, because these are presumed to be less costly to produce.

This leads to the question of the adaptive value of small drone production. During the reproductive season of *A mellifera* in Germany the percentage of small drones in a 'natural' (non-manipulated) drone congregation area in Germany is about 9% (Berg, 1991). The presence and production of large drones decreases at the end of the mating season. The production of small drones, however, will continue often throughout the brood rearing period. Insufficiently mated queens and laying workers (in queenless colonies) lay unfertilized eggs in worker cells and small drones will be reared that meet less competition from large drones before or after the season. Queen loss or mortality during these periods will result in emergency queen cells and young queens that may be the main target for small drones. Small drones might thus exploit mating opportunities outside the limited temporal window of the short mating season.

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Résumé — Taille corporelle et succès reproductif des mâles d'abeilles (*Apis mellifera* L). On a étudié sur un lieu de rassemblement de mâles (LRM) la répartition des mâles de la race *A m carnica* en fonction de leur taille et de leur succès reproductif. Des mâles de petite taille ont été élevés dans des cellules d'ouvrières, alors que les mâles de grande taille provenaient des cellules de mâles (tableau III). La mutation récessive cordovan (cd) a été utilisée comme marqueur génétique. Tandis que les mâles (+) présentaient une couleur du corps foncée, les mâles (cd) étaient reconnaissables à leur coloration brun clair. Les recherches ont porté sur deux années consécutives au cours desquelles on a fait varié la composition de la population de mâles (tableau I). Pour établir la répartition des deux types de mâles sur le LRM on a procédé régulièrement à des captures (fig 2). On n'a pas noté de différence significative dans la répartition tant dans l'espace (horizontalement et verticalement) que dans le temps des deux types de mâles sur le LRM (tableaux IV, V et VI).

Des reines vierges homozygotes (cd/cd) ont été introduites à proximité du LRM et ont effectué leur vol de fécondation au-dessus de celui-ci. Les ouvrières issues de ces reines ont été classées en fonction de la couleur de leur corps, caractéristique qui permet de connaître la fréquence d'accouplement (tableau II). La comparaison de l'analyse de la descendance avec la composition des mâles sur le LRM a donné les résultats suivants (tableau VI) : i) les petits mâles ont un succès reproductif moindre que les gros mâles ; ii) les gros mâles (cd) ont un avantage reproductif vis-à-vis des gros mâles (+). Les gros mâles ne se différencient des petits ni par la durée de vol, ni par la répartition sur le LRM, ni par la quantité de sperme produit; leur supériorité reproductrice pourrait être due au fait qu'il réussissent mieux lors de la concurrence pour l'approche de la reine au cours du vol de fécondation. Ceci conduit à poser la question de la valeur adaptative de la production de mâles de petite taille. Le pourcentage de petits mâles au sein d'une population naturelle de mâles sur un LRM en Allemagne est d'environ 9 %. (Berg, 1991). Les petis mâles, qui sont produits durant toute la période de couvain, pourraient avoir de l'importance avant le début et à la fin de la période de fécondation, moments où la présence et la production des gros mâles diminue fortement. La concurrence étant moindre, les petits mâles pourraient alors jouer un rôle dans la fécondation des reines issues de cellules royales de supersédure (en dehors de la période de fécondation).

Apis mellifera / mâle / taille corporelle / succès reproductif / analyse de descendance

Zusammenfassung — Körpergröße und Reproduktionserfolg von Drohnen (_Apis mellifera_ L). Die Verteilung von Drohnen der Rasse *Apis mellifera carnica* unterschiedlicher Körpergröße auf einem Drohnensammelplatz (DSP) und ihr Reproduktionserfolg wurden untersucht. Kleine Drohnen wurden in Arbeiterinnenzellen erzeugt, während große Drohnen aus Drohnenzellen stammten (Tabelle III). Zur genetischen Markierung wurde die Mutante Cordovan (cd) eingesetzt, die eine klare Klassifizierung vor Ort ermöglicht. Während (+) Drohnen eine dunkle Körperfarbe zeigten, waren (cd) Drohnen an ihrer hellbraunen Färbung kenntlich. Die Untersuchungen wurden in zwei aufeinanderfolgenden Jahren, mit unterschiedlichen Drohnenzusammensetzungen durchgeführt (Tabelle I). Die Verteilung der beiden Drohnentypen auf dem DSP wurde durch kontinuierliche Fänge festgestellt (Abb 2). Es gab keine signifikanten Unterschiede in der horizontalen, vertikalen und der zeitlichen Präsenz der Drohnentypen auf dem DSP (Tabelle IV, V und VI).

Jungfräuliche homozygote (cd/cd) Königinnen flogen auf den DSP zum Hochzeitsflug. Die von diesen Königinnen produzierten Arbeiterinnen wurden entsprechend ihrer Körperfarbe klassifiziert, wodurch Aussagen zur Paarungsfrequenz möglich waren (Tabelle VII). Der Vergleich der Nachkommenschaftsanalyse mit der Drohnenzusammensetzung auf dem DSP erbrachte folgende Ergebnisse: 1) Kleine (+) Drohnen hatten einen geringeren reproduktiven Erfolg als große (cd) Drohnen; 2) Große (cd) Drohnen hatten einen reproduktiven Nachteil gegenüber großen (+) Drohnen. Nachdem sich die kleinen und die großen Drohnen weder in der Flugzeit, noch in ihrerVerteilung auf dem Drohnensammelplatz oder in der Zahl der von ihnen produzierten Spermien unterschieden, könnte die festgestellte reproduktive Überlegenheit der großen Drohnen auf einer erfolgreicheren Konkurrenz beim Anflug auf die Königin beruhen. Dies führt zur Frage des adaptiven Wertes der Produktion von kleinen Drohnen. Der Anteil von kleinen Drohnen an der natürlichen Drohnenpopulation auf einem DSP in Deutschland betrug ca. 9% (Berg 1991). Der über die gesamte Brutzeit produzierte Typ von kleinen Drohnen könnte vor Beginn und gegen Ende der Paarungssaison von Bedeutung sein, wenn das Vorhandensein und die Produktion der großen Drohnen stark abnimmt. Bei verminderter Konkurrenz könnten dann u.U. kleine Drohnen vor allem bei der Paarung von Königinnen aus Nachschaffungszellen (außerhalb der Paarungssaison) eine Rolle spielen.

Apis mellifera / Drohne / Körpergröße / Reproduktionserfolg / Nachkommenschaftanalyse

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