

The flight characteristics of drones in relation to mating

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ABSTRACT

Flight characteristics of drones were compared to workers, and sometimes queens, to gain insight into the evolved design of drones with respect to mating opportunity and competitiveness. Drones had inferior flight endurance and range as compared to workers, but similar maximum flight speed and maneuverability, indicating these characteristics have limited significance for drone fitness. Drones had superior kinetic energy, which might provide an advantage in aggressive encounters between males, but such encounters have not been observed. Drones had much greater total force production, which might allow drones to carry queens during mating. The evolution of drone size is still a mystery, though this study suggests that investigators should pursue further research into lift force and the potential for intermale mate competition.

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Apis mellifera, queen, drone, flight, mating

INTRODUCTION

In spite of the fact that honey bees (*Apis mellifera* L.) have been domesticated for over 7,000 years (Crane 1975), many aspects of their biology are unknown. The dearth of information is especially acute for drones, which have traditionally been ignored, perhaps because of their lack of commercial value and simplified social behavior relative to workers, queens and whole colonies. In this study I address a perennial issue: why are drones so large? I use information integrated from studies of drone flight physiology and honey bee mating behavior to gain insight into the potential for either sexual selection or natural selection to have influenced the evolution of drone size in honey bees. This area has suffered from a lack of direction and lack of data, probably because of the difficulty of observing natural mating. Such information is needed to address a number of pending questions. For example, African drones may be smaller than European drones (Rinderer *et al.* 1985), but we have almost no idea what effect this may have on the potential for hybridization.

It is clear that drones have not evolved to work. They are poorly equipped for foraging, having rather small mandibles, proboscis and honey crop (Snodgrass 1925). Drones do not forage, but fuel their mating flights by taking stored honey (Orosi-Pal 1959). Drones also do not perform tasks within the hive, lacking wax glands and most of the pheromone-producing and nutritional glands (see review by Winston 1987).

Drone morphology is consistent with their almost exclusive involvement in reproductive behavior. They have extremely large eyes, which occupy most of the head, and very sensitive antennae, which have 10 times the number of antennal plate organs as workers (Winston 1987). These are used in locating and orienting to flying virgin queens (see Currie 1988 for review). Success in mating is very likely to be the primary selection pressure on drones. However, it is not always clear what characteristics of drones must be optimized in order to maximize reproductive fitness. A brief review of honey bee mating behavior may allow some insight into these questions.

Mature drones take flight during the afternoon in suitable weather. There may be large numbers of drones at drone congregation areas or on flight paths leading to and from them (Loper *et al.* 1987), so the operational sex ratio at these sites is very skewed toward drones. If a virgin queen appears the drones pursue her as a swarm known as a "comet" (Gary 1963, Koeniger 1986a).

If insemination is successful, the tip of the endophallus breaks off, the drone becomes paralyzed immediately, falls to the ground, and soon dies (Ruttner 1956, Gary 1963, Koeniger *et al.* 1979); therefore, a drone can mate only once. Because mating opportunities are rare, this limitation is probably not significant. Nonetheless, selection pressure on drones must be intense.

Because mating occurs in flight, drone characteristics must be consistent with maximization of flight performance. Few attempts to address these questions have been made (except see Starr 1984). This study examines drone flight performance characteristics, in-

cluding those that may affect mating opportunity (the endurance and range of flight) and competitiveness (flight velocity [V], kinetic energy [Ek], maneuverability, and load-carrying capacity). I have measured some of these attributes directly, others I took from the available literature. By comparing drone performance with that of workers and queens, it should be possible to understand how drone characteristics affect performance, and to gain insight into how the morphology and physiology of drones has evolved in relation to flight and mating.

FLIGHT ENDURANCE AND RANGE

A drone should be able to increase the probability of encountering a queen by increasing the duration and range of a mating flight. Energy-efficient flight and large fuel storage would reduce transit time and refueling time at the hive because drones must derive all the energy for a mating flight from honey obtained at the hive and carried in the honey crop. Such characteristics would also be consistent with selection for flight range, which might be important since the finite distance covered by drones from a given colony limits the ability of the queen from that colony to spread her genes (Taylor and Rowell 1988).

The fuel-carrying capacity of drones was determined by measuring the volume of honey carried in the honey crop. Drones were collected as they left the hive, taken to the laboratory, and dissected. These individuals were assumed to be sexually mature drones departing on mating flights, having filled their honey crops from colony stores. The honey crop was removed intact and weighed. Since the contribution of the thin-walled membrane of the crop itself is negligible, the entire mass was assumed to be honey.

Honey bee flight is fueled aerobically by carbohydrate metabolism (Beenackers 1969, Kammer and Heinrich 1978, Beenackers *et al.* 1984, Nachtigall *et al.* 1989, Rothe and Nachtigall 1989) through rapid uptake of sugars from midgut to hemolymph (Crailsheim 1988). Therefore, an oxycaloric equivalent for carbohydrate of 478 kJ/mol O₂ was assumed (Gnaiger 1983). Using oxygen consumption data from published sources (Coelho 1991a) and assuming 18.1 J/ml honey (White 1975), the average theoretical mating flight times of drones were calculated. The average flight time of workers was calculated in the same way, assuming a modest honey crop volume of 25 mL, although the maximum is considerably higher (Sylvester *et al.* 1983, Schmid-Hempel *et al.* 1985).

The calculated average flight times were multiplied by flight speed (Coelho 1991a and below) divided by two to generate theoretical flight ranges, distances that drones and workers should be able to travel if they flew straight away from the hive and back.

Twelve drones leaving the hive averaged 215.8 ± 3.0 mg (mean ± SE) body mass (Mb), and 16.1 mg honey crop contents with a maximum of 30 mg. The reproductive tract weighed 27.8 ± 1.0 mg. Based on these fuel reserves and rate of utilization described above, a drone should be able to fly for an average of ~37 min at a thorax temperature (T_{th}) of 40°C. These estimates are

consistent with measured rates of food consumption (Mindt 1962, as cited by Ruttner 1966, Berg 1988, as cited by Nachtigall *et al.* 1989). A worker carrying 25 mg of honey in its crop should be able to fly continuously for 105 min, almost three times longer than a drone. The theoretical flight range of a drone with an average honey crop load and average flight speed is 6.0 km. The range of a worker is 38.2 km at average speed and crop load, over 6 times that of a drone.

Most studies show that the average length of time spent in a mating flight by a drone is ~30 min. (reviewed by Witherell 1971), which represents 81% of the theoretically available time. Drones routinely reach congregation areas 5 km from the natal colony, and occasionally as far as 6 km, while virgin queens probably fly only 2-3 km on mating flights (Ruttner and Ruttner 1966). Yet matings routinely occur between drones and queens whose natal colonies are 12 km apart, and occasionally up to 17 km apart (Taylor, Kinsolver, and Otis 1986). Drones return from mating flights with virtually empty honey crops (Ruttner 1966, Coelho, unpublished observations). These observations suggest that drones commonly use all of the time and range available to them from their energy stores, perhaps retaining a small amount of fuel as a safety factor. The energetic strategy of drones appears to be that of utilizing nearly completely the energy stores on a given flight, returning to the hive, refueling, then taking another flight. In this way as many as eight flights may be taken in one day (Witherell 1971). Workers should be able to fly for a much longer period of time than drones, though they seldom do in reality (Gary 1975). These considerations make it unlikely that drones are designed for endurance. Similarly, flight range must not be the key drone character for if drones were subject to strong selection for maximal flight range they would be designed more like workers—with smaller body mass, greater fuel reserves, and faster flight.

FLIGHT SPEED

Koeniger (1986b) suggested that the fastest drone reaches the queen first and copulates with her. Since drones are larger and have a higher body temperature, one might expect them to be able to fly faster than workers. Hence, flight speed might provide the evolutionary driving force for drone size. Although this scenario is intuitively appealing, the data do not support it.

Flight speed values for drones and workers were taken from Coelho (1991a), and kinetic energy was calculated for drones and workers from values of Mb and V therein. Mean V for drones (5.28 ± 0.10 m/s) is significantly lower than that of workers (5.85 ± 0.08 m/s) as measured by K-band radar (Coelho 1991a). The maximum speed is similar for drones and workers, ~8 m/s.

Because V is more strongly correlated with T_{th} than with body mass (Coelho 1989) and drones have higher T_{th} (Coelho 1991a, 1991b), one would predict that they should be faster flyers than workers. The fact that this is not the case indicates that drones have not evolved large body size and high T_{th} simply as a means of improving V.

Table 1

Calculated kinetic energy of a drone and worker of average mass at mean and maximal flight speed.

	Kinetic Energy (J)	
	Drone	Worker
at mean flight speed	2.88	1.85
at maximum flight speed	6.48	3.24

Note: mean body mass of drone = 0.2 g, worker = 0.1 g.
Mean flight speed of drone = 5.37 m/s, worker = 6.08 m/s.
Maximal speed for both = 8 m/s.

KINETIC ENERGY

Male-male competition could provide an alternative adaptive characteristic for drones. The ability to knock aside a rival drone that is attempting to mount the queen and to then supplant the rival's position depends upon the usurping drone imparting sufficient kinetic energy to the incumbent drone. Kinetic energy (E_k) during flight is related to body mass and flight speed according to a standard Newtonian equation:

$$E_k = 0.5M_bV^2$$

The kinetic energy of a drone and worker of average mass at mean and maximal V were calculated from published values of M_b and V (Coelho 1991a) and are presented in Table 1. In each case E_k is substantially higher in the drone.

The mean E_k of drones used in flight speed experiments was 3.25 ± 0.27 J, which falls between the mean and maximal theoretical values for drones, and is much greater than the mean value for workers.

In spite of their lower flight speed, drones generate a great deal of kinetic energy during flight as compared to workers, mostly because drones are larger. These considerations would imply that drones are well suited to aggressive, contact interactions with other drones. Unfortunately, there is no evidence that they actually engage in such interactions. Direct aggressive interaction among drones attempting to mate with tethered or artificial queens has not been observed, even with the use of high speed films (Gary 1963, Koeniger 1986b, Coelho and Taylor 1994). Such contact would likely cause injury, decreasing the odds of successful mating.

MANEUVERABILITY

It is possible that maneuverability is important in determining drone mating success. With an operational sex ratio so heavily skewed to males, and the obvious potential for competition, maneuvering for access to the queen could provide the opportunity to mate. Ma-

neuverability can be defined as the ability to accelerate and decelerate. Acceleration is equal to force divided by mass; therefore, the acceleration of a flying insect is equal to the force that it generates in flight divided by its body mass, or mass-specific force production. Thus, an index of maneuverability can be determined by measuring maximal force production (F_{max}) and body mass.

F_{max} is largely determined by flight muscle mass, so that a crude index of maneuverability is the ratio of flight muscle mass to body mass (flight muscle ratio, or FMR, [Marden 1987]).

The force produced by drones, workers, and queens was taken from Coelho (1991b). On average drones produce an F_{max} (3.95 ± 0.23 mN) over twice that of workers (1.73 ± 0.13 mN). Mass-specific F_{max} was not significantly different between workers and drones. Queens produced an F_{max} intermediate between that of workers and drones, but generated a mass-specific F_{max} significantly lower than that of the other two groups.

Drones have higher FMR than queens, and as a result have higher mass-specific F_{max} (Coelho 1991b). Drones should, therefore, have sufficient maneuverability to catch a flying queen, and variation in maneuverability may have important consequences for the mating success of drones. Drones also had higher FMR than workers, but mass-specific F_{max} was similar between the two. These results make it unlikely that drone size has evolved solely in response to selection for maneuverability during mating, for it should be less expensive for a colony to produce the same number of small drones as large drones, and both would have the same maneuverability.

LIFT FORCE

It is possible that absolute force production is more important for drone mating success than mass-specific force production. Since F_{max} is strongly related to size (Coelho 1991b), drones are well constructed for it. During mating the drone approaches the flying queen

from below, and mounts her from above, grasping her by the abdomen with all six legs (Gary 1963, Koeniger *et al.* 1979). It may be that the drone then carries the queen in flight, although direct observations of natural mating are not available to support or contradict this possibility. Copulation occurs only after the queen voluntarily opens the sting chamber, so that the drone may have to carry the queen for more than several seconds (Gary 1963). Drone-queen pairs can fly freely without losing altitude (Gary 1963), and drones can carry a 148.5 mg weight in flight—approximately that of a queen (Betts 1939).

The force required to lift a drone and a typical virgin is 3.4 mN (Coelho 1991b). Drones can produce 3.95 mN under optimal thermal conditions. Thus a drone of average size need generate only 86% of F_{max} to lift himself and a queen. The reverse cannot occur—a queen cannot lift a drone and herself, for the queen at best produces only 2.15 mN of force (Coelho 1991b). Perhaps this is why on rare occasions a queen and dead drone in copula are observed after falling to the ground (Jordan 1954, Ruttner 1956, Gary 1963). Normally the explosive force of ejaculation results in the separation of the dead drone from the queen (Gary 1963). If this mechanism fails the queen cannot support the sum of the drone's mass and her own, and falls.

For a queen to be carried aloft by a worker, 2.56 mN of force are required. This is far above the force a worker is capable of producing, 1.73 mN (Coelho 1991b). Total maximum force is strongly correlated with all measures of size. Hence, the large size of drones may be a result of selection for absolute force production during flight—the ability to carry a queen. If so, then the support of large external loads is required. Internal loads are, therefore, minimized: drones have low semen volume (Harbo 1986) and honey crop volume, even though these shortcomings result in brief flight time, short flight range, and limited gamete delivery.

In an interesting contrast, workers have large honey crops, but seldom fill them completely when foraging, an apparent constraint of energetic efficiency and lifespan (Schmid-Hempel *et al.* 1985, Schmid-Hempel and Wolf 1988, Wolf and Schmid-Hempel 1989). Hence, selection pressure for additional lift capacity in workers is likely to be slight. Workers need not be any larger, at least for the purpose of foraging.

CONCLUSION

I have attempted to identify key flight characteristics for which drones are adapted. In that all organisms represent a compromise among numerous selection pressures, it seems likely that the flight design of drones is a compromise among several needs, including perhaps all of those mentioned above and others. Nonetheless, fruitful avenues of research might focus on some of these areas, especially lift force and male-male competition.

It is somewhat surprising that so little work of this nature has been done. The idea that selection for queen-carrying resulted in the evolution of large drones is at least 120 years old. Darwin (1871) suggested that "...amongst the Bees, the males of *Apis mellifica*...are

larger than the females. The explanation of this anomaly is that a marriage flight is absolutely necessary with these species, and the male requires great strength and size in order to carry the female through the air."

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