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Scientific note

A scientific note on a trend towards bivoltinism in Western North American bumblebees

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Bumblebees, *Bombus* spp. (Hymenoptera: Apidae), are eusocial insects that require a continuous supply of floral resources for colony growth and development (Alford 1975). In temperate regions, mated over-wintered queens emerge in early spring, forage for pollen and nectar, establish nests, and lay a series of eggs. Subsequently, workers emerge, forage, and the colony grows. During late summer, if adequate floral resources are available in the landscape, the colony increases considerably in size. At the end of the colony life cycle, reproductives, namely males and new queens, are produced. These exit the nest, and mate, after which males die and the queens seek over-wintering sites for diapause. Thus, the colony life cycle typically extends for 3–5 months with worker foraging activity coinciding with spring- or summer-blooming plants (Heinrich 1979). Consequently, bumblebees in temperate regions have one generation a year, while with continuous availability of foraging resources, tropical species produce several generations a year (Sakagami 1976). However, some temperate species appear to undergo more than one generation in a year. Workers of *Bombus terrestris* (L.) have been observed foraging throughout the year in England (Stelzer et al. 2010), Tasmania (Buttermore 1997), Corsica (Rasmont and Adamski 1996), New Zealand (Donovan and Weir 1978), and Sardinia (Krausse 1910a, b), suggesting that a second generation is produced in the same year. Similar observations were reported for *Bombus jonellus* (Kirby) in Norway (Meidell 1968; Douglas 1973) and for *Bombus pratorum* (L.) and *Bombus hortorum* (L.) in England (Sladen 1912). Here, we present the first report of a trend towards bivoltinism in three temperate bumblebee species, all in the subgenus Pratobombus, in the Willamette Valley of western Oregon in western USA, based on the following studies.

Over the past 6 years, we have surveyed *Bombus* spp. intensively in this region, and have observed queens of *Bombus vosnesenskii* Radoszkowski, *Bombus mixtus* Cresson, and *Bombus melanopygus* Nylander foraging as early as January to February and workers as late as September to October. Given that colony life cycles typically extend less than 5 months in temperate regions (Heinrich 1979), the presence of workers of these three species over 8 months in Oregon suggests the occurrence of a second generation. In 2008 and 2009, we serendipitously observed nest initiation behavior in queens of *B. vosnesenskii* that emerged in summer from colonies placed on a field stand in June of each year adjacent to a field of flowering red clover (*Trifolium pratense* L.; Fabaceae). In both years, all workers and queens in each of the colonies used in the study were marked on the thorax with distinct colored tags (Betterbee, Greenwich, NY, USA) for monitoring colony development and foraging behavior. Colonies were surveyed daily to determine emergence of workers and queens. Queens were distinguished from workers based on their emergence from queen pupae and on their large body size. During July of 2008, unexpectedly, from three of the ten colonies, we observed three newly emerged queens displaying typical nest initiation behaviors in small cavities

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located near to, but outside of, their natal nest. They collected pollen, constructed both pollen and nectar storage cells, laid eggs, and incubated the egg clumps. The queens recruited one to two large-sized workers from their original colony to aid in nest initiation, behavior that is typically observed in tropical species (Sakagami 1976).

In 2009, a new set of eight colonies were initiated from wild queens collected in spring, and subsequently placed in the field, one colony produced a new queen. This queen also displayed nest initiation behaviors including the formation of pollen and nectar storage cells, egg laying, incubation of brood, and recruitment of a worker from the natal nest, in small cavities located outside of her original nest. During both years, nest-founding behavior was, however, disrupted when colonies had to be removed from the field because of red clover seed harvest operations. We do not know if the three new queens produced in 2008 and the one in 2009 were mated.

During June of 2010, one wild colony each of *B. vosnesenskii*, *B. mixtus*, and *B. melanopygus* were transferred to the lab and reared for another study. In each of these colonies, we observed similar trends towards bivoltinism. In August, a total of 30 *B. vosnesenskii*, 7 *B. mixtus*, and 15 *B. melanopygus* queens emerged from a single colony of each species. After emergence, all queens were placed with males for mating, and subsequently moved to nest boxes after 24 h. Queens were not forced to forego diapause, nor were they exposed to any of the common lab manipulation techniques used in commercial rearing to mimic diapause in lab-reared queens. However, queens were provided with a worker from their natal nest as is typically done for facilitating nest initiation (Kwon et al. 2006). Within a week, all of the queens of all three species initiated nests by constructing nectar storage pots, laying eggs, and incubating egg clumps. Each of the 7 colonies initiated by *B. mixtus* queens and the 15 colonies by *B. melanopygus* produced workers (ranging from 7 to 25 and from 6 to 23, respectively), and males (ranging from 1 to 5 and from 2 to 4, respectively). The 30 colonies of *B. vosnesenskii* produced only males (ranging from 5 to 14). We speculate that the absence of workers produced from the *B. vosnesenskii* colonies was due to the lack of mating under laboratory conditions. There are no published reports of successful mating in *B. vosnesenskii* under laboratory conditions; perhaps, this species needs a larger space than what we provided for adequate flight prior to and during mating than what the other species required.

We believe that the observations described above provide evidence of a trend towards bivoltinism rather than examples of colonies being usurped by workers from the same or other colonies. Workers can get broody when the original queen dies and no longer produces the pheromones or engages in the behaviors that suppress ovary development in workers (van Honk et al. 1980; Roseler et al. 1981). However, in our field study, the original queen was alive when the newly emerged individuals (which we referred to as queens) were broody. Secondly, broody workers typically lay eggs within the natal nest (Duchateau and Velthuis 1989), while the queens of *B. vosnesenskii* that emerged near the red clover field laid eggs in cavities outside of their natal nest. In addition, when workers get broody, other workers will assist them in nest initiation but subsequently eat a large proportion of the newly laid eggs (Duchateau and Velthuis 1988). This did not happen in our study. Finally, when we reared wild colonies of *B. mixtus* and *B. melanopygus* in the lab, the queens that emerged mated and initiated new colonies producing both workers and males without first going through diapause. Typically, for colony initiation by queens reared in the laboratory, they are exposed to cold storage or carbon dioxide to stimulate them to lay eggs without undergoing a period of diapause (Horber 1961; Tasei 1994).

For temperate bumblebees to develop a second generation in a year, the presence of floral resources is critical. In two studies conducted on *B. jonellus* in Norway, abnormally mild and dry summers over 2 years were believed to be responsible for queens producing two brood cycles in each season (Meidell 1968; Douglas 1973). We speculate that the trend towards production of a second generation exhibited by *B. vosnesenskii*, *B. mixtus*, and *B. melanopygus* in our studies is due to the presence of an abundance of red clover bloom towards the end of summer in the Willamette Valley. Legumes are considered to be important for development of bumblebees, and their recent absence in landscapes in Europe has been attributed as a factor leading to declines in bumblebee species (Goulson et al. 2005). Thus, bumblebee species in the Willamette Valley may benefit from the late-blooming red clover crop not only for colony development during the period that males and new queens are produced (Rao and Stephen 2010) but also for development of a second generation. Further research is needed to assess the extent of bivoltinism in *B. vosnesenskii*, *B. mixtus*, and *B. melanopygus* in the Willamette Valley, and to determine whether other bumblebee species in the region, and in other regions in North America, exhibit the same trend.

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Note Scientifique: tendance au bivoltinisme chez des bourdons de l'ouest des Etats-Unis

Eine wissenschaftliche Notiz über einen Trend zum Bivoltinismus bei Hummeln im westlichen Nordamerika

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