

DANCING WITH CARNIOLAN BEE

PLEŠEMO S KRANJSKO ČEBELO

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ABSTRACT

Dancing with carniolan bee

Slovene heritage in beekeeping is based on knowledgeable bee management practice documented well in 18th century. Well described mating biology of honeybees was first detailed description of specific behavior of honeybees based on observation in well know subspecies of Carniolan bee. Later in 20th century special focus was on dance communication, which was described by VON FRISCH (1965) as a dance language. In the work alone it was not described as a special cognitive capability of the honeybees but rather instinctive highly specialized behavior pattern. From original work to nowadays many detailed studies of the dance communication were published and also used as a tool to study orientation and learning during foraging behavior. New concept have been involved, especially in sense of new views and methods in cognitive science. How much cognition is involved in foraging behavior of honeybees depends on how wide we accept definition of cognition.

Key words: *Apis mellifera carnica*, communication, waggle dance, recruitment, foraging, information transfer

IZVLEČEK

Plešemo s kranjsko čebelo

Slovenska čebelarska dediščina temelji na dobrem poznavanju čebelarske prakse, ki je bila dokumentirana že v 18. stoletju. Dobro opisana biologija parjenja medonosne čebele je bil prvi podroben opis posameznega vedenja medonosne čebele temelječe na opazovanjih dobro poznane podvrste kranjske čebele. Kasneje v 20. stoletju je bila posebna pozornost na plesnem sporazumevanju čebel, ki jo je opisal VON FRISCH (1965) kot čebelji jezik. V samem njegovem delu sicer ni bilo opisano kot posebna razumska zmožnost čebel ampak bolj kot močno usmerjen nagonski vedenjski vzorec. Od originalnega dela pa do danes je bilo objavljenih veliko podrobnih raziskav plesnega sporazumevanja in tudi uporabljeno kot orodje za raziskavo orientacije in učenja med pašnim vedenjem. Razvili so se novi koncepti, še posebej v smislu novih pogledov in metod v kognitivni znanosti. Koliko razuma je vključeno v pašno vedenje čebel je odvisno od tega, kako na široko sprejmemo definicijo razuma.

Ključne besede: *Apis mellifera carnica*, sporazumevanje, zibajoči ples, novačenje, paša, prenos informacije

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1 INTRODUCTION

Many researchers around the world use specifically Carniolan bee (*Apis mellifera carnica* Poll. 1879) for their research. These were more typically in the past when majority of bee research activities were in Europe, also pioneering research in dance communication in honeybees. Nowadays, scientist are using bee dance as a tool to learn more about biology, especially foraging behavior of honeybees (DYER 2002; CHITTKA 2004). We learned a lot about sensory capability, orien-

tation and learning of bees using observation of dancing bees and their attendance. Modern science is trying to dig into cognitive capability of the bees with the help of dancing behavior (MENZEL & GIURFA 2001; MENZEL 2012; CHITTKA 2017). These developments put under investigation basic questions about dance communication: What are mechanisms of information transfer? What kind of learning is involved and how is that combined with fixed behavior pattern? We will



Figure 1: Carniolan bee (*Apis mellifera carnica*) on flowers of *Hacquetia epipactis*, which is common spring flowering plant in beech forest in Slovenia and some neighboring geographic areas. This plant species from the family of Apiaceae got genus name from Balthasar Hacquet who worked together with Antonio Scopoli in Idria for few years from 1766. This picture symbolize early scientific reports about bees from homeland of Crniolan bee (photo: J. Božič). (<https://www.slovenska-biografija.si/oseba/sbi554298/#slovenski-biografski-leksikon>)

Slika 1: Kranjska čebela (*Apis mellifera carnica*) na cvetju tevja (*Hacquetia epipactis*), ki je običajna pomladi cvetoča rastlina bukovih gozdov Slovenije in nekaterih sosednjih geografskih območij. Ta rastlinska vrsta iz družine kobulnic (Apiaceae) je dobila rodovno ime po Baltasarju Hacquetu, ki je delal skupaj z Antonom Scopolijem v Idriji nekaj let od leta 1766. Slika simbolizira zgodnja znanstvena poročila o čebelah iz rodne dežele kranjske čebele (foto: J. Božič). (<https://www.slovenska-biografija.si/oseba/sbi554298/#slovenski-biografski-leksikon>)

start with historical involvement of Carniolan bee in behavior research, continue with pioneering work in dance communication, development of first controversy, modern studies of information transfer and potential developments of new controversies related with dance communication in honeybees and how to override it with fruitful scientific research.

Carniolan bee was the most frequent used subspecies in detailed behavior observations

Carniolan bee was spread around the world mainly from county Carniola of former Austria- Hungarian Imperium (later part of Yugoslavia and nowadays Slovenia) in second half of 19th and first half of 20th cen-

tury (GNILSAK 2003; ŠALEHAR & GREGORI 2011). Slovenian beekeepers were not known only because of interesting bees that they managed, but also for good beekeeping practice (GREGORI ET AL. 2003). In 18th century that was recognized by Austrian court, where Slovenian beekeeper Anton Janša started teaching beekeeping in established beekeeping school. He also wrote a book with details about honey bee colonies reproduction with emphasizes on management of swarming behavior (JANŠA 1771). There he described in detail also matting of queens outside of the hive with multiple drones during several mating flights of young queens before they start laying eggs. That was general knowledge (ŠALEHAR 2015). Even several years earlier was written by Scopoli (Figure 1) in his book *Entomologica Carniolica*, that queen is mated



Figure 2: Carniolan bee on the buckwheat flower. Buckwheat was regular and wide spread pasture of late summer for honeybees in time of A. Scopoli and A. Janša. It enabled well developed overwintering colonies with well established honey stores, two important predispositions for good early spring bee colonies development (photo: J. Božič).

Slika 2: Kranjska čebela na cvetu ajde. Ajda je bila redna in razprostranjena paša čebel poznega poletja v času A. Scopolija in A. Janše. Omogočila je dober razvoj prezimovalnih družin z dobro oblikovanimi rezervami medu, dve ključni predpostavki za dober zgodnji pomladni razvoj čebeljih družin (foto: J. Božič).

in the air (SCOPOLI 1763). That experienced well documented beekeeping in 18th century (Figure 2) built up foundation for later development of massive breeding of Carniolan bees to sheep around the world bee swarms and queens. Carniolan bee become the second most frequent subspecies that is used in commer-

cial bee hives (CRANE 1990). In central and western Europe Carniolan bee replaced authentic dark bee *Apis mellifera mellifera* which led to the use of Carniolan bees in the most of the research performed in Europe regarding bee biology and especially bee behavior.

2 DANCE COMMUNICATION

Also Karl von Frisch started with Carniolans in Graz and continued latter also in Germany with the same subspecies studying intriguing behavior of foraging bees, which he latter described in detail and called it "Tanzsprache" (Dance language) (VON FRISCH 1965).

His laureated work with Nobel price (VON FRISCH 1974) introduced naming of behavior in a sense of better exception by general public and also to get more

attention also by scientific community. Basically it is communication behavior pattern, which codes information about direction and distance of the food source. Coding is not made in the sense of language but rather of linear adjustment of the few parameters of the fixed action patten based on the experience of the foraging bee. So it is better to name it dance communication then dance language (ROSIN 1978).

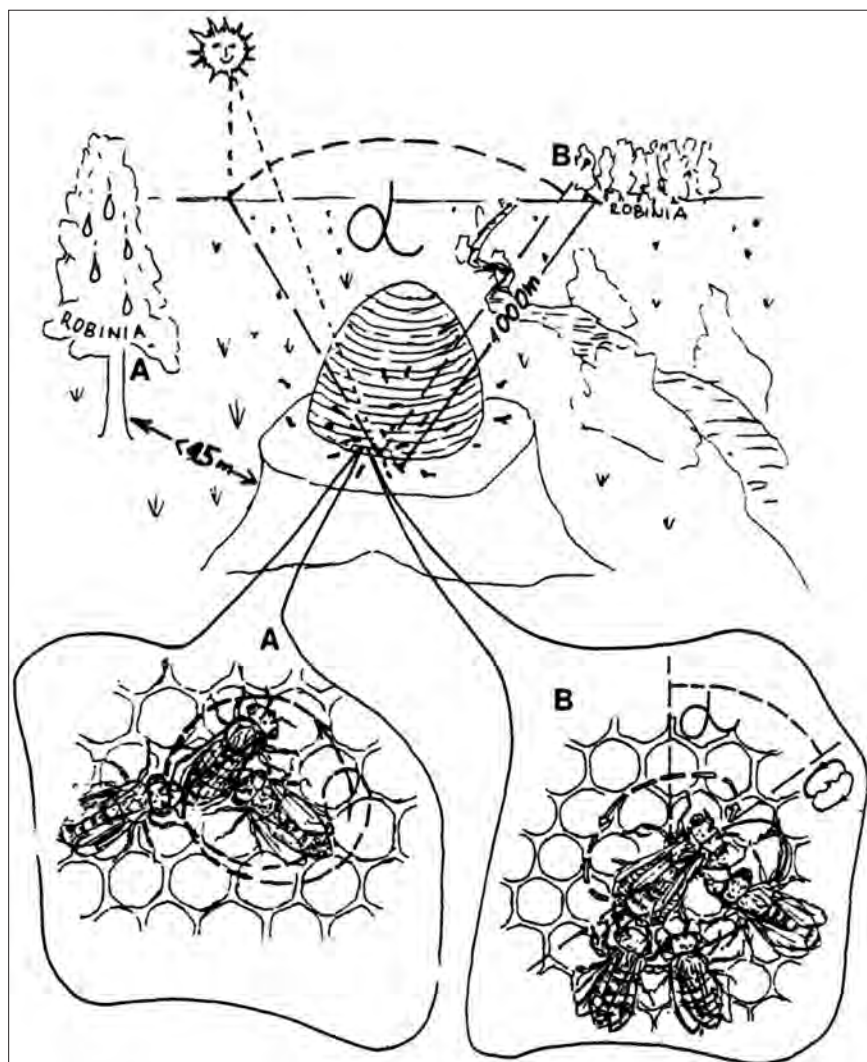


Figure 3: Two types of dances of foraging bees were originally described, round dance (A) and waggle dance (B) (von Frisch 1965). Drawing from (Božič 1988). Slika 3: Originalno sta bila opisana dva plesa pašnih čebel, krožni (A) in zibajoči ples (B) (von Frisch 1965). Risba iz (Božič 1988).

Von Frisch detailed description

It took one quarter of century to find out whole decoding value of dance behavior of foraging bees inside of the hive (VON FRISCH 1923; VON FRISCH 1946). Initial observations of dancing behavior related it to special excitement or arousal of foraging bees with no specific information content (BUTTEL-REEPEN 1915 in VON FRISCH 1965). It was soon noticed that circle dance is related to short distance of the source and waggle dance to long distance (VON FRISCH 1923). Later it has been recognized as a potential way to more efficiently spread olfactory signals related to the foraging site. Not earlier than in 1940's have been described potential coding of food source in the pattern of the dance behavior regarding to distance and direction (VON FRISCH 1946). Karl von Frisch recognized that orientation of the dancer's wagging path (waggle run) in figure eight pattern is related to the orientation of the food source from where she arrived (Figure 3). Coding is related to the angle between the food source and horizontal projection of the sun direction which is

translated into the angle between the waggle run and vertical direction on the comb in the dark hive (Figure 3). The distance has even simpler correlation, farther is the forage longer is waggle run. Waggle run can be also observed as number of waggles that are performed during the run and even whole dance cycle, waggle run plus return run to start new waggling can be related to the distance of forage (VON FRISCH 1965). It is important to note that return runs are going interchangeable to the left and right side of the direction of waggle run. This stereotype change in path could be important in establishing potential followers that are in the position to pick up dance information (BOŽIČ & VALENTINČIČ 1991, Figure 4). Further investigations of details in dance performance revealed some interesting differences between subspecies of *Apis mellifera* and also between different species of genus *Apis*. From the focus of this paper I'd like to point out some earlier observations that showed Carniolan bee (*A. mellifera carnica*) as most distant foraging tuned subspecies (VON FRISCH 1965). There has been recognized also the only existing difference between Carniolan bee and



Figure 4: Wagging dancer in the middle with the follower on her left side pushing its antennae into dancer's abdomen (photo: J. Božič).

Slika 4: Zibajoča plesalka v sredini s sledilko na njeni levi strani, ki potiska tipalnice v zadek plesalke (foto: J. Božič)

other subspecies in the change of circle dance into waggle dance. This uniqueness has been studied also genetically (JOHNSON ET AL. 2002). It looks like there exist genetic basis although exact gene involved in that is not known yet. One recent study of Carniolan and dwarf bee colonies arise some doubt in all studies of racial and species differences summarized in K.von Frisch book (SEN SARMA ET AL. 2004).

Emergence of controversy, olfactory hypothesis

Well documented research of waggle dance communication didn't completely convinced the whole research community. There had been developed alternative hypothesis for recruitment of bees. Adrian Wenner was the leader in opponent research and clearly demonstrated that bees can be well recruited by olfactory signals alone (WENNER ET AL. 1969; MUNZ 2005). With his help and involvement of some philosophers waggle dance communication become a key example how scientific controversy develops and how hard is to resolve it (ROSIN 1978; WENNER & WELLS 1990). One of the most important obstacle in researchers thinking is postulating teleological hypothesis. In fact most reports started with preposition that dance communication is working and enable information transfer about reported sources. Among hundreds of scientific papers are only few that are actually experimentally testing recruitment success of the bees that came into position to pick up dance information (WENNER ET AL. 1967; MAUTZ 1971; GOULD 1975a; GOULD 1975b; JUDD 1994; ABRAMSON & BOŽIČ 2004; TANNER & VISSCHER 2009). In all of them can be justified critics done by Wenner that olfactory hypothesis was not taken into account in the design of the experiment (WENNER ET AL. 1969). Most close to the proper experimental setup was Gould with the redirection of the followers by the dancer to different location that actually dancers danced (GOULD 1975a). That is possible if the dancers have covered ocelli which causes increase of threshold when the bees are oriented toward light source instead of gravitation on vertical comb. In that way dancers oriented their dances according to gravity but the followers recognize direction according to the light source, which was rotated for specific angle. Although ingeniously designed experiment from technical point of view missed proper control that would dismissed olfactory hypothesis experimentally tested by Wenner and coworkers. Such developments in research of dance communication results in statements that scientists write their believes even not thoughts about hypothesis (ROSIN 1978).

Searching additional modalities for information transfer

After partially resolved problem between Wenner's olfactory and von Frisch's dance language hypothesis (VADAS 1994; KIRCHNER & GRASSER 1998; MUNZ 2005), most of the research were further focused to potential channels for communication signals' transfer and orientation capabilities of the bees. Although many findings related to the orientation of the bees were well summarized by the von Frisch, it was not very clear how bees actually use sun compass during search of the food and successful returning into the hive. In 80's we got very detailed behavior model for sun compass in honeybees (ROSSEL & WEHNER 1986; CHENG & FREAS 2015). At that time were known more in detail also physiological background in polarized light detection by bees. One of the most significant finding is that bees must have internal compass that is aligned with the external polarized pattern. They can achieve that during circling in orientation phase of flight. This is one of the key finding that can help a lot in explaining of the recruitment behavior of the bees, which I will interpret latter in the manuscript. One of the most fruitful direction was study of the sounds produced by the waggle dancers. Although first observations of the dance sound were done by Esch (1961) and nearly at the same time by Wenner (1962) in a time of von Frisch preparation of the synthesis of dance language hypothesis. In the new wave of the sound research lead by Axel Michelsen made detailed description of the sound field around the dancer and even showed that bees could detect those signals in close approach (MICHELSEN ET AL. 1986; MICHELSEN ET AL. 1987; KIRCHNER ET AL. 1988). With mechanical robot bee they tried to recruit bees by artificial produced signals (MICHELSEN ET AL. 1992). They did get some recruits but in the view of Wenner's research bees were able to find the experimental location through olfactory cues. Researchers, fascinated by their results, hypothesized that sound is a main channel for dance signals transfer from the dancer to the potential recruits. In this case they count all bees in the dancer's vicinity as a potential recruits.

Details of behavior patterns around the dancer – clue to understanding of dance information transfer?

Meanwhile I studied behavior of all bees in the dancers surroundings and find out that we can clearly distinguish followers and attenders (BOŽIČ & VALENTINČIČ

1991). The follower has to move with the dancer at list two waggle runs and that is possible only in close approach which actually enables direct contacts by the vibrating and wagging dancer's abdomen. Also recruitment experiments showed that following is linked to the recruitment success, but it shouldn't be too long (ABRAMSON & BOŽIČ 2004). That means it is more likely that the recruit before final leaving of the hive, when was successful in finding communicated food source, followed fewer waggle runs in one attempt than during previous sessions inside of the hive. Around the dancers we can detect passing by bees with no special attention to the dancer's behavior, there could be occasional observers that are only once evoked to orient toward the dancer or better signals that she emits. There are attenders which stood around the dancer, typically at list one waggle run, oriented to the dancer, but hardly to be able to move along the dancer. These are potential followers that can jump into the dancer's vicinity and follow them for at list two waggle runs. We could say that there are typically two behavior patterns of the bees in the dance field, dancing and following. Dancing is performed by foragers after arrival into the hive. Not all foragers are dancing. There should be specific arousal due to quality of food source and stimulation of hive bees. During experiments on artificial feeders we can observe that a scout bee (first time forager) does not necessary dance

during the first arrival (ABRAMSON & BOŽIČ 2004). It can be observed that they can be even too much aroused. They are moving vigorously, exchanging food with the nestmates and do short shivering dance with no specifically oriented stereotypical pattern that is observed in waggle dance. Sometimes they stay in the hive for longer time but more often they leave it very soon and then they could perform waggle dance after next arrival. We could say that there should be specific level of arousal regarding forage quality that waggle dance can be initiated after touches of bees when the forager moves with specific tempo across the hive. After several visits arousal drops down below the threshold that enables stimulations by the hive bees to trigger waggle dance. They still share the food and immediately leave the hive. They are still well motivated for foraging activity. That is also indication of relative stable arousal for foraging activity. This classical ethological approach is missing more support from the neurophysiological data. There are recent attempts to identify neural networks that are involved in direction and distance information processing by the foraging bee (STONE ET AL. 2017). There have been observed some differences between dancers and followers in brain regions regarding biogenic amine contents and contents of their metabolites (BOŽIČ & WOODRING 1998; BARRON ET AL. 2007). From early results we could say that higher number and stronger correla-

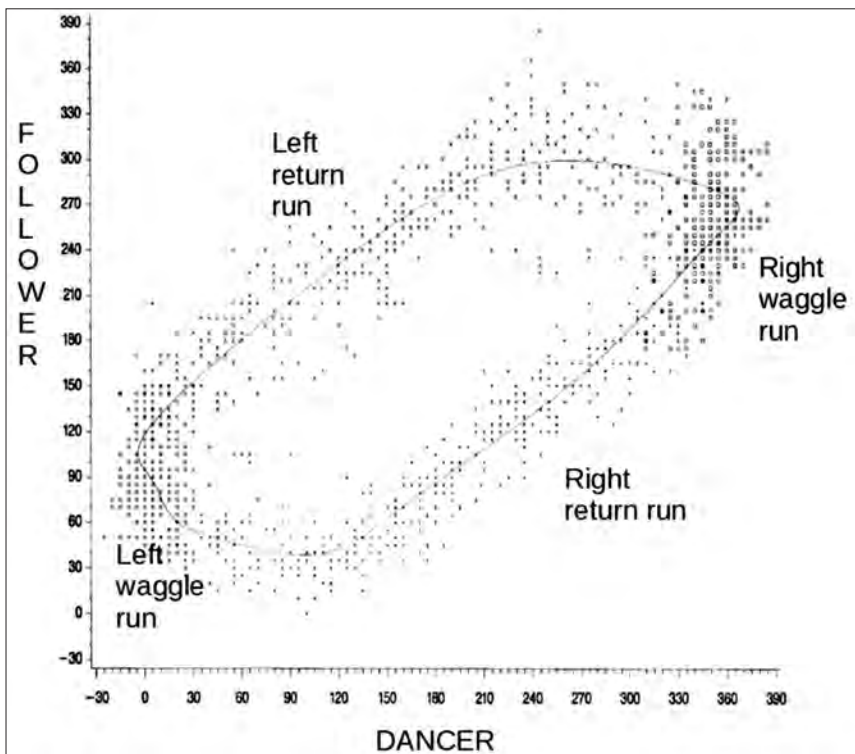


Figure 5: Dependence of follower's body angle from the orientation of the dancer's body through all phases of waggle dance. Polynomial regression line represents 9 dances observed with 14 followings and 2294 positions measured in the rate of 5/s. Adapted from (Božič 1992). Slika 5: Odvisnost kota položaja sledilke od orientacije telesa plesalke skozi vse faze zibajočega plesa. Polinomska regresijska linija predstavlja 9 opazovanih plesov s 14 sledenji in 2294 položajev izmerjenih s pogostostjo 5/s. Prilagojeno po (Božič 1992).

tions might be indicators of activation and coordination of specific neuronal networks in honeybee brain. Identification of this networks is difficult in direct way, because classical neurophysiological approach is hard to apply. That was very successful to learn a lot about learning in bees, where bees can be fixed, performed behavior experiment and also using electrodes for recording nerve signals and to label them (MENZEL & GIURFA 2001; MENZEL 2012). To get comparable data in free flying bees it is just time to come reality. More about that at the end.

I've just touch motivation as one of the classical ethological term that is used to describe ability of the animals to perform behavior patterns. Most often can be related hormonal regulation to the motivational states, at list as an import precondition that is needed that some kind of behavior orientation can be expressed. In case of honey bee foraging it has been shown that onset of foraging activity is related to higher levels of juvenile hormone (FAHRBACH & ROBINSON 1996). It was mainly recognized as a maturation factor that directs specific development of the honeybee brain. Part of this regulation is also maturation of subesophageal gland that starts producing enzyme alpha glucosidase for sucrose cleavage. Both can be observed using biochemical methods (radio-labeled synthesis rate of JH and enzyme test for subesophageal gland). It is interesting that there have been found indications that followers, potential recruits have JH synthesis rate in the range of foragers, but hive resting bees in much lower range (BOŽIČ & WOODRING 2000). That could be one indication that followers, future foragers have to be mature to be able to forage.

Recruitment success and recruitment dynamic, maturation and learning

Maturation enforced by JH might go enough fast that bees that starts attending and following of the dancers can be successful recruits on the next day. Also during the same day we might be able to observe active followers, even exiting the hive, but they are not making to the location communicated inside of the hive. In most of recruitment and related papers, researcher try to interpret unsuccessful flights as fail in message transfer (MAUTZ 1971; TAUTZ 1996; TANNER & VISSCHER 2009). For such experiments Wenner would use it as another proof for olfactory hypothesis. Although understanding that during experimentation most of the recruits are naive foragers (design of the experiments, e.g. marking bees at hive entrance) and not redirected existing foragers, we should take a note that they are

actually in the process of maturation into regular foragers. Similar processes have been observed in field crickets (STOUT ET AL. 1991). Also, if bees didn't forage for a while it might be redirected to some hive activities and has to be motivated again for foraging activity. This process needs some time. It might be directed to proper sensitivity of the neuronal networks which are involved in information transfer and food search. Another possible reason even for former foragers could be that bees are not just flying to communicated location, but they are actually searching new food site after stimulation inside of the hive. That also Wenner said and mentioned that followers after leaving of the hive are actually making circling flights similar to orientation flights during first flight outside of the hive (WENNER 1967). We did observe that as well and see that circling is typical behavior of the follower after leaving the hive (PLIBERŠEK 2002). What could that mean? Following of the dancer is instinctive behavior triggered after approach to the aroused forager inside of the hive. This behavior synchronization enables sharing olfactory stimuli from the dancer, which after some food sharing in the dance field can be interpreted as classical conditioning of the future forager, which can be interpreted as explicit learning of foraging signals (BITTERMAN ET AL. 1983). Along that the follower moves with the dancer which is most likely connected with some kind of latent learning of the forage direction and distance (Figure 5). The direction is somehow stored in latent learning memory, well connected with detection of sun compass (MENZEL ET AL. 2001; CAHILL ET AL. 2001). Roots of that might be searched even in solitary wasps, nesting inside of dark cavities, where they have to orient themselves based on gravitational fields to return to their nest where they store collected insects or spiders for future young (BROCKMANN 1980; ZEIL 1993; STÜRZL ET AL. 2016). They also do have well established orientation based on latent learning of objects near nest sites and most likely for longer foraging paths also connected with some compass. Gravitational orientation and sun compass orientation had been linked somehow during evolution of genus *Apis* (GOULD & TOWNE 1987; DORNHAUS & CHITTKA 1999). Newer view on evolution of genus *Apis* suggests that its development actually started with nesting in cavities and not outside and also regarding to that evolves waggle dance in genus *Apis* (KOTTHOFF ET AL. 2013), but that was not taken in account by newer reviewers (AVARGUÈS-WEBER ET AL. 2015; BARRON & PLATH 2017). Researchers mainly see waggle dance as food source locator, but evolutionary it might be even more important as a nest site locator then foraging site. If it evolved first really as a nest site locator would be intriguing

scientific hypothesis to solve. Distance information didn't seem to be so complicated as direction information. But, we can read in von Frisch's book many environmental and even internal factors that affect the generation of signals related to the distance (VON FRISCH 1965). Most of the research invoked an explanation based on some kind of energetic level, longer distance more energy is spent and a different way of perception of that by bees. Already these early studies gave some hints that visual experience of the bees might play an important part of the perception of distance. Detailed research decades later showed that actually the use of some kind of visual odometer that is based on optic flow in the visual field of the flying, even waking bees (SRINIVASAN ET AL. 1997; SRINIVASAN ET AL. 2000). That was successfully manipulated in the experiments providing different speeds of visual feed around flying bees. As I suggested, direction is perceived with some kind of latent learning, also distance seems to be communicated in a similar way.

Wenner was right that olfaction is a primer clue to find a food source. Bees are conditioned to the smells of the brought food, not only due to touching the dancer, but also due to food exchange in the region of the comb where dances are performed. In general, conditioned learning is accepted as explicit learning, which directly guides animals according to the conditioned signal to perform related behavior. In our case, foraging is a part of feeding behavior continued outside of the hive due to high excitement by signals brought by the foragers. If they find a strong flow of a specific smell learned inside of the hive, they would choose that path as shown by Wenner (WENNER ET AL. 1969). But not all available paths of smell are equal. Bees could find valuable pasture also in the direction where winds are blowing and taking away from the hives specific smells of the pasture. So bees can't find a proper smell path and they are searching in front of the hives during circling wider and wider around the hive. Here they can take part in latent learned information about the direction. The bee is suddenly switched from a circle type of flight to more or less straight flight at least for a while. My interpretation is that during the circling bees are scanning the sky and when the direction excitation in the field of internal e-vectors of a polarized pattern aligns with latent "imprinted" direction during following the dancer that stops circling search and continues in straight search. We know that this is not perfectly straight flight. Occasionally bees do additional circling on the so-called straight flight. That can be recognized through close dots from radar images of recruited bees (RILEY ET AL. 2005; LANDGRAF ET AL. 2018). Also in that case they might repeat searching

and are switched again in a straight line. And how far are bees doing that? Here comes in play distance information. Distance information keeps enough high arousal for straight flight that it is possible to reach the communicated site. Researchers observed that bees don't reach typically on the first exit of the hive the communicated location (MAUTZ 1971; WENNER ET AL. 1991). As I already mentioned here, it can come into account maturation in our game of recruitment, but not only that, also a proper arousal of foraging neural pathways that bees are able to reach the communicated distance. When bees finally reach the right distance they still search for the food, most likely mainly on olfactory cues, because they don't have other information about the food site that might be released during performing dance in the hive. Perhaps the existence of many different food smells around the dance field in the hive might make searching even tougher at the reached location. So, at the end we can say von Frisch was right, too, but only in a sense of communicating dance information but not in using language. That was argued already (ROSIN 1978) and seems pretty clear, although modern scientists still use the term language because it is better heard by the general public? *Short conclusion could be that recruitment is based on conditionally learned olfactory signals that are searched outside of the hive. This instinctive searching behavior is guided in a latent way by dance information obtained inside of the hive as described above.*

Subspecies specifics in dance code

Communication of the distance information is the only major difference that can be observed between subspecies inside of *Apis mellifera*. Comparisons of the waggle run time and related signals in dance patterns between different subspecies reveal that the Carniolan bee is on one extreme side with the best steep curve of dependency regarding the distance of the communicated location (BOCH 1957). It is also interesting that two closely related subspecies, Italian (*Apis mellifera ligustica*) and Carniolan (*Apis mellifera carnica*), have one of the largest differences. It is an open question if that could be a partial barrier for admixing of these two subpopulations of honeybees. In the last century it was observed a strong effect of the Carniolan bee on the population of Italian bees in Northern Italy (RÚA ET AL. 2009; MARINA D MEIXNER ET AL. 2009), but only minor in Slovenia as the closest neighbor with the Carniolan bee, where we could expect a similar effect of Italian bees on the Slovenian part of the Carniolan bee population (SUŠNIK ET AL. 2004). In recent decades that can be explained with management of



Figure 6: Bees in the swarm, time for collective decision for new home location (Photo: J. Božič).
Slika 6: Čebele v roju, čas za skupinsko odločitev za novo lokacijo doma (Foto: J. Božič)

bees, special care in Slovenia for authentic population and no similar program in Northern Italy for Italian bee. Old reports about subspecies didn't report major mixed area (RUTTNER 1988; COMPARINI & BIASIOLO 1991). Perhaps minor differences in dance communication could lead to lower fitness in mixed colonies if they have some problems in communicating colony resources. Perhaps forage is not so critically as finding new nesting site during swarming (Figure 6). Colony in the swarm has to establish enough high quorum regarding new nesting site, before they are leaving temporal resting location close to mother site (JAYCOX & PARISE 1980; SEELEY & TOWNE 1992; SCHMIDT 1995; CAMAZINE ET AL. 1999; SEELEY & VISSCHER 2004; PASSINO & SEELEY 2006). It might be possible that departure of the swarm would be delayed if enough high quorum can not be achieved. Different translation of the distance information could result in wrong search location by the bees that try to re-find communicated new nest site. That means that bees could spent too much food reserve during the resting and searching and have worse possibilities to successfully start building new comb at new location. That bees could have problem with the departure as it was shown during observation of extreme situation when two swarms were mixed together during take off and were not able to establish straight flight to new location (personal observation). They sit down together on lower branch and tried to fly away again, but with no success. They

tried that several times but at the end, when was at the lowest branch, they were captured in a new hive. Since swarming is the unit of genetic reproduction in honeybees that could be one of the potential mechanism to achieve partial separations of the two populations, but that has to be experimentally verified. It has been shown that observed difference in waggle run that relates to the distance interpretation, change for circle run into waggle run is coded with one locus (RINDERER & BEAMAN 1995; JOHNSON ET AL. 2002). That doesn't necessary mean that that specific locus is directly related to the pattern of the dance but rather to the specific arousal of the neuron network that is involved in expression of waggle runs. Some research suggests that change from circling to waggling is not change from A to B behavior but rather continuum from simple circling to perfect waggle runs (KIRCHNER *et al.* 1988). That support idea that there might be only tiny genetic change that is related to the specific behavioral arousal as described above. Dance tempo related to the distance might define also geometric possibility for change from circle runs to waggle runs. What exactly is that genetic base we don't know yet, but it could be something common with observed other behavior differences between Italian and Carniolan bees as well typical difference in colorization of cuticle. All recent attempts were not able to find specific functional genomics difference between this two subspecies of honeybee.

3 PERSPECTIVES FOR FUTURE RESEARCH

Functional genetic difference is just one opened question that needs to be solved in future to find out what makes essential difference between two closely related subspecies of honeybees. Along with recognized more calm behavior of Carniolan bee, the dance pattern is one of more exact difference that can be checked between populations. Some recent research gave some clues, but more molecular mining is needed and experimental testing to solve that opened question. It might drag along some other not yet explained observed differences between respected subspecies of honeybees.

Signals' processing in the brain of honeybee is more clear than ever (DYER *et al.* 2011; MENZEL 2012; ZELLER *et al.* 2015; HELD *et al.* 2016; STONE *et al.* 2017). Although specific stereotyped patterns of signals have not been tested and that could be big adventure in future neurophysiology research in honeybee. Some progress can be done with new experiments with fixed

bees in the lab, but the key experiments is needed with free flying bees. In the past were some attempts to have mounted electronic devices on the back to monitor specific brain activity (PICKARD & WELBERRY 1976; BRILL ET AL. 2014). Miniaturization of electronic devices and use of radio-frequency identification technology (DE SOUZA ET AL. 2018; NUNES-SILVA ET AL. 2018), even building small computers inside of the tags on the thorax of the bee gives definitely new possibilities to monitor behavior during active flight (SULEIMAN ET AL. 2018). Classical behavior experiments are still welcome and it looks like researchers are not encouraged to repeat innovative experimental design to collect more data and especially in better controlled conditions. One of such experiment is Gould redirection of the recruits to different site that was actually reported by the dancers (difference in change to orient directly to light by followers and dancers) (GOULD 1975a). Additionally we need more quantitative docu-

mentation of searching behavior of the followers after leaving the hive (PLIBERŠEK 2002) and also some kind of manipulation of searching behavior using different foraging sites according to sun direction. In this review I propose that combined model from olfactory and dance language hypothesis is realistic and can be

improved with taking in account that new recruits need to mature for foraging as well to be properly aroused to fulfill needs regarding available energy for flight and capability to process efficiently information during searching of new forage after excited leave of the hive based on following the dancer.

4 REFERENCES

- ABRAMSON C. I. & BOŽIČ J., 2004: *Multiple search flights of the dancer's followers: result of information or energy deficiency*. *Apiacta* 38: 358–365.
- AVARGUÈS-WEBER A., LIHOREAU M., ISABEL G. & GIURFA M., 2015: *Information transfer beyond the waggle dance: observational learning in bees and flies*. *Frontiers in Ecology and Evolution* 3: a24. doi: 10.3389/fevo.2015.00024.
- BARRON A. B., MALESZKA R., MEER R. K. V. & ROBINSON G. E., 2007: *Octopamine modulates honey bee dance behavior*. *Proceedings of the National Academy of Sciences* 104/5: 1703–1707. doi: 10.1073/pnas.0610506104.
- BARRON A. B. & PLATH J. A., 2017: *The evolution of honey bee dance communication: a mechanistic perspective*. *Journal of Experimental Biology* 220/23: 4339–4346. doi: 10.1242/jeb.142778.
- BITTERMAN M. E., MENZEL R., FIETZ A. & SCHÄFER S., 1983: *Classical conditioning of proboscis extension in honeybees (*Apis mellifera*)*. *Journal of Comparative Psychology* 97/2: 107–119. doi: 10.1037/0735-7036.97.2.107.
- BOCH R., 1957: *Rassenmässige Unterschiede bei den Tänzen der Honigbiene (*Apis mellifica* L.)*. *Zeitschrift für vergleichende Physiologie* 40/3: 289–320. doi: 10.1007/BF00340572.
- BOŽIČ J., 1988: *Dogajanja med cebeljim plesom - analiza vedenja sledilke : diplomska naloga*. Ljubljana : [J. Božič].
- BOŽIČ J., 1992: *Socialne interakcije pasnih čebel v panju : magistrska naloga = Social interactions of honeybees in hive*. Ljubljana : [J. Božič].
- BOŽIČ J. & VALENTINČIČ T., 1991: *Attendants and followers of honey bee waggle dances*. *Journal of Apicultural Research* 30/3–4: 125–131. doi: 10.1080/00218839.1991.11101246.
- BOŽIČ J. & WOODRING J., 1998: *Variations of brain biogenic amines in mature honeybees and induction of recruitment behavior*. *Comparative Biochemistry and Physiology-Part A: Molecular & Integrative Physiology* 120/4: 737–744.
- BOŽIČ J. & WOODRING J., 2000: *Variation in JH synthesis rate in mature honeybees and its possible role in reprogramming of hypopharyngeal gland function*. *Pflügers Archiv European Journal of Physiology* 439/7: 163–164.
- BRILL M. F., REUTER M., RÖSSLER W. & STRUBE-BLOSS M. F., 2014: *Simultaneous Long-term Recordings at Two Neuronal Processing Stages in Behaving Honeybees*. *Journal of Visualized Experiments : JoVE* /89 doi: 10.3791/51750.
- BROCKMANN H. J., 1980: *Diversity in the Nesting Behavior of Mud-Daubers (*Trypoxylon politum* Say; Sphecidae)*. *The Florida Entomologist* 63/1: 53–64. doi: 10.2307/3494656.
- CAHILL L., MCGAUGH J. L. & WEINBERGER N. M., 2001: *The neurobiology of learning and memory: some reminders to remember*. *Trends in Neurosciences* 24/10: 578–581. doi: 10.1016/S0166-2236(00)01885-3.
- CAMAZINE S., VISSCHER P. K., FINLEY J. & VETTER R. S., 1999: *HOUSE-HUNTING BY HONEY BEE SWARMS: collective decisions and individual behaviors*. *Insectes Sociaux* 46/4: 348–360.
- CHENG K. & FREAS C. A., 2015: *Path integration, views, search, and matched filters: the contributions of Rüdiger Wehner to the study of orientation and navigation*. *Journal of Comparative Physiology A* 201/6: 517–532. doi: 10.1007/s00359-015-0984-9.
- CHITTKA L., 2004: *Dances as Windows into Insect Perception*. *PLOS Biology* 2/7: e216. doi: 10.1371/journal.pbio.0020216.
- , 2017: *Bee cognition*. *Current Biology* 27/19: R1049–R1053. doi: 10.1016/j.cub.2017.08.008.
- COMPARINI A. & BIASIOLO A., 1991: *Genetic discrimination of Italian bee, *Apis mellifera ligustica* versus Carniolan bee, *Apis mellifera carnica* by allozyme variability analysis*. *Biochemical Systematics and Ecology* 19/3: 189–194. doi: 10.1016/0305-1978(91)90002-H.
- CRANE E., 1990: *Bees and beekeeping: science, practice and world resources*. *Bees and beekeeping: science, practice and world resources*. .

- DORNHAUS A. & CHITTKA L., 1999: *Insect behaviour: Evolutionary origins of bee dances*. Nature 401/6748: 38. doi: 10.1038/43372.
- DYER A. G., PAULK A. C. & RESER D. H., 2011: *Colour processing in complex environments: insights from the visual system of bees*. Proceedings of the Royal Society B: Biological Sciences 278/1707: 952–959. doi: 10.1098/rspb.2010.2412.
- DYER F. C., 2002: *The Biology of the Dance Language*. Annual Review of Entomology 47/1: 917–949. doi: 10.1146/annurev.ento.47.091201.145306.
- ESCH H., 1961: *Über die Schallerzeugung beim Werbetanz der Honigbiene*. Zeitschrift für vergleichende Physiologie 45/1: 1–11. doi: 10.1007/BF00297754.
- FAHRBACH S. E. & ROBINSON G. E., 1996: *Juvenile Hormone, Behavioral Maturation, and Brain Structure in the Honey Bee*. Developmental Neuroscience 18/1–2: 102–114. doi: 10.1159/000111474.
- VON FRISCH K., 1923: *Über die "Sprache" der Bienen, eine tierpsychologische Untersuchung*. Zool Jb Physiol 40: 1–186.
- , 1946: *Die Tänze der Bienen*. Oest. Zool. Z. 1/1/2: 1–48.
- , 1965: *Tanzsprache und Orientierung der Bienen*. Berlin; Heidelberg; New York : Springer.
- , 1974: *Decoding the Language of the Bee*. Science 185/4152: 663–668.
- GNILSAK I., 2003: *Kranjska cebela = The Carniolan bee : tradicija in dediscina v sodobnem cebelarstvu na Sloven-skem = tradition and heritage in modern beekeeping in Slovenia : zbornik Cebelarskega muzeja*. Radovljica : Muzeji radovljiske občine.
- GOULD J. L., 1975a: *Honey Bee Recruitment: The Dance-Language Controversy*. Science 189/4204: 685–693.
- , 1975b: *Communication of distance information by honey bees*. Journal of comparative physiology 104/2: 161–173. doi: 10.1007/BF01379457.
- GOULD J. L. & TOWNE W. F., 1987: *Evolution of the Dance Language*. The American Naturalist 130/3: 317–338. doi: 10.1086/284713.
- GREGORI J., POKLUKAR J., MIHELČ J. & STARMAN B., 2003: *The Carniolan bee (Apis mellifera carnica) in Slovenia : a gift to beekeepers of the world on the occasion of the Apimondia Congress in Ljubljana, Slovenia, 2003*. Lukovica : Beekeepers' Association of Slovenia.
- HELD M., BERZ A., HENSGEN R., MUENZ T. S., SCHOLL C., RÖSSLER W., HOMBERG U. & PFEIFFER K., 2016: *MICRO-GLOMERULAR SYNAPTIC COMPLEXES in the Sky-Compass Network of the Honeybee Connect Parallel Pathways from the Anterior Optic Tubercle to the Central Complex*. Frontiers in Behavioral Neuroscience 10 doi: 10.3389/fnbeh.2016.00186.
- JANŠA A., 1771: *Abhandlung vom Schwärmen der Bienen*. Wien : Gedruckt bey Joseph Kurzböck ...
- JAYCOX E. R. & PARISE S. G., 1980: *Homesite Selection by Italian Honey Bee Swarms, Apis mellifera ligustica (Hymenoptera: Apidae)*. Journal of the Kansas Entomological Society 53/1: 171–178.
- JOHNSON R. N., OLDROYD B. P., BARRON A. B. & CROZIER R. H., 2002: *Genetic Control of the Honey Bee (Apis mellifera) Dance Language: Segregating Dance Forms in a Backcrossed Colony*. Journal of Heredity 93/3: 170–173. doi: 10.1093/jhered/93.3.170.
- JUDD T. M., 1994: *The waggle dance of the honey bee: Which bees following a dancer successfully acquire the information?* Journal of Insect Behavior 8/3: 343–354. doi: 10.1007/BF01989363.
- KIRCHNER W. H. & GRASSER A., 1998: *The Significance of Odor Cues and Dance Language Information for the Food Search Behavior of Honeybees (Hymenoptera: Apidae)*. Journal of Insect Behavior 11/2: 169–178. doi: 10.1023/A:1021098405564.
- KIRCHNER W. H., LINDAUER M. & MICHELSEN A., 1988: *Honeybee dance communication*. Naturwissenschaften 75/12: 629–630. doi: 10.1007/BF00366482.
- KOTTHOFF U., WAPPLER T. & ENGEL M. S., 2013: *Greater past disparity and diversity hints at ancient migrations of European honey bee lineages into Africa and Asia*. Journal of Biogeography 40/10: 1832–1838. doi: 10.1111/jbi.12151.
- LANDGRAF T., BIERBACH D., KIRBACH A., CUSING R., OERTEL M., LEHMANN K., GREGGERS U., MENZEL R. & ROJAS R., 2018: *Dancing Honey bee Robot Elicits Dance-Following and Recruits Foragers*. arXiv:1803.07126 [cs]
- MARINA D MEIXNER, CECILIA COSTA, PER KRYGER, FANI HATJINA, MARIA BOUGA, EVGENIYA IVANOVA & RALPH BÜCHLER., 2009: *Conserving diversity and vitality for honey bee breeding*. Journal of Apicultural Research 2010/49(1): 85–92. doi: 10.3896/IBRA.1.49.1.12.
- MAUTZ D., 1971: *Der Kommunikationseffekt der Schwänzeltänze bei Apis mellifica carnica (Pollm.)*. Zeitschrift für vergleichende Physiologie 72/2: 197–220. doi: 10.1007/BF00297822.

- MENZEL R., 2012: *The honeybee as a model for understanding the basis of cognition*. Nature Reviews Neuroscience 13/11: 758–768. doi: 10.1038/nrn3357.
- MENZEL R. & GIURFA M., 2001: *Cognitive architecture of a mini-brain: the honeybee*. Trends in Cognitive Sciences 5/2: 62–71. doi: 10.1016/S1364-6613(00)01601-6.
- MENZEL R., MANZ G., MENZEL R. & GREGGERS U., 2001: *Massed and Spaced Learning in Honeybees: The Role of CS, US, the Intertrial Interval, and the Test Interval*. Learning & Memory 8/4: 198–208. doi: 10.1101/lm.40001.
- MICHELSSEN A., ANDERSEN B. B., STORM J., KIRCHNER W. H. & LINDAUER M., 1992: *How honeybees perceive communication dances, studied by means of a mechanical model*. Behavioral Ecology and Sociobiology 30/3: 143–150. doi: 10.1007/BF00166696.
- MICHELSSEN A., KIRCHNER W. H. & LINDAUER M., 1986: *Sound and vibrational signals in the dance language of the honeybee, Apis mellifera*. Behavioral Ecology and Sociobiology 18/3: 207–212. doi: 10.1007/BF00290824.
- MICHELSSEN A., TOWNE W. F., KIRCHNER W. H. & KRYGER P., 1987: *The acoustic near field of a dancing honeybee*. Journal of Comparative Physiology A 161/5: 633–643. doi: 10.1007/BF00605005.
- MUNZ T., 2005: *The Bee Battles: Karl von Frisch, Adrian Wenner and the Honey Bee Dance Language Controversy*. Journal of the History of Biology 38/3: 535–570. doi: 10.1007/s10739-005-0552-1.
- NUNES-SILVA P., HRNCIR M., GUIMARÃES J. T. F., ARRUDA H., COSTA L., PESSIN G., SIQUEIRA J. O., DE SOUZA P. & IMPERATRIZ-FONSECA V. L., 2018: *Applications of RFID technology on the study of bees*. Insectes Sociaux doi: 10.1007/s00040-018-0660-5.
- PASSINO K. M. & SEELEY T. D., 2006: *Modeling and analysis of nest-site selection by honeybee swarms: the speed and accuracy trade-off*. Behavioral Ecology and Sociobiology 59/3: 427–442.
- PICKARD R. S. & WELBERRY T. R., 1976: *Printed circuit microelectrodes and their application to honeybee brain*. Journal of Experimental Biology 64/1: 39–44.
- PLIBERŠEK T., 2002: *Polet pasne cebele (Apis mellifera carnica) iz panja : diplomska naloga : univerzitetni studij = Flight of forager bee (Apis mellifera carnica) from the hive : graduation thesis : university studies*. Ljubljana : [T. Pliberšek].
- RILEY J. R., GREGGERS U., SMITH A. D., REYNOLDS D. R. & MENZEL R., 2005: *The flight paths of honeybees recruited by the waggle dance*. Nature 435/7039: 205–207. doi: 10.1038/nature03526.
- RINDERER T. & BEAMAN L., 1995: *Genic control of honey bee dance language dialect*. Theoretical and applied genetics 91/5: 727–732.
- ROSLIN R., 1978: *The honey bee “language” controversy*. Journal of Theoretical Biology 72/4: 589–602. doi: 10.1016/0022-5193(78)90273-4.
- ROSSEL S. & WEHNER R., 1986: *Polarization vision in bees*. Nature 323/6084: 128–131. doi: 10.1038/323128a0.
- RÚA P. D. LA., JAFFÉ R., DALL’OLIO R., MUÑOZ I. & SERRANO J., 2009: *Biodiversity, conservation and current threats to European honeybees*. Apidologie 40/3: 263–284. doi: 10.1051/apido/2009027.
- RUTTNER F., 1988: *Biogeography and taxonomy of honeybees*. Biogeography and taxonomy of honeybees. .
- ŠALEHAR A., 2015: *Praha matice s troti v zraku, izvirno slovensko odkritje najstarejše kronološko urejene objave*. Ljubljana : samozal.
- ŠALEHAR A. & GREGORI J., 2011: *Obstoja pa ena pridna in utrjena čebela, taka je kranjska*. Ivančna Gorica; Brdo pri Lukovici : Regijska zveza Petra Pavla Glavarja ; Čebelarstva zveza Slovenije, Javna svetovalna služba v čebelarstvu.
- SCHMIDT J. O., 1995: *Dispersal Distance and Direction of Reproductive European Honey Bee Swarms (Hymenoptera: Apidae)*. Journal of the Kansas Entomological Society 68/3: 320–325.
- SCOPOLI G. A., 1763: *Ioannis Antonii Scopoli ... Entomologia Carniolica: exhibens insecta Carnioliae indigena et distributa in ordines, genera, species, varietates, methodo Linnaeana*. Vindobonae : typis Ioannis Thomae Trattner ...
- SEELEY T. D. & TOWNE W. F., 1992: *Tactics of dance choice in honey bees: do foragers compare dances?* Behavioral Ecology and Sociobiology 30/1: 59–69. doi: 10.1007/BF00168595.
- SEELEY T. D. & VISSCHER P. K., 2004: *Quorum sensing during nest-site selection by honeybee swarms*. Behavioral Ecology and Sociobiology 56/6: 594–601. doi: 10.1007/s00265-004-0814-5.
- SEN SARMA M., ESCH H. & TAUTZ J., 2004: *A comparison of the dance language in Apis mellifera carnica and Apis florea reveals striking similarities*. Journal of Comparative Physiology A 190/1: 49–53. doi: 10.1007/s00359-003-0470-7.
- DE SOUZA P., MARENDY P., BARBOSA K., BUDI S., HIRSCH P., NIKOLIC N., GUNTORPE T., PESSIN G., DAVIE A., DE SOUZA P., MARENDY P., BARBOSA K., BUDI S., HIRSCH P., NIKOLIC N., GUNTORPE T., PESSIN G. & DAVIE A., 2018: *Low-Cost Electronic Tagging System for Bee Monitoring*. Sensors 18/7: 2124. doi: 10.3390/s18072124.

- SRINIVASAN M. V., ZHANG S., ALTWEIN M. & TAUTZ J., 2000: *Honeybee Navigation: Nature and Calibration of the "Odometer."* *Science* 287/5454: 851–853. doi: 10.1126/science.287.5454.851.
- SRINIVASAN M., ZHANG S. & BIDWELL N., 1997: *Visually mediated odometry in honeybees.* *Journal of Experimental Biology* 200/19: 2513–2522.
- STONE T., WEBB B., ADDEN A., WEDDIG N. B., HONKANEN A., TEMPLIN R., WCISLO W., SCIMECA L., WARRANT E. & HEINZE S., 2017: *An Anatomically Constrained Model for Path Integration in the Bee Brain.* *Current Biology* 27/20: 3069–3085.e11. doi: 10.1016/j.cub.2017.08.052.
- STOUT J., ATKINS G. & ZACHARIAS D., 1991: *Regulation of cricket phonotaxis through hormonal control of the threshold of an identified auditory neuron.* *Journal of Comparative Physiology A* 169/6: 765–772. doi: 10.1007/BF00194904.
- STÜRZL W., ZEIL J., BOEDDEKER N. & HEMMI J. M., 2016: *How Wasps Acquire and Use Views for Homing.* *Current Biology* 26/4: 470–482. doi: 10.1016/j.cub.2015.12.052.
- SULEIMAN A., ZHANG Z., CARLONE L., KARAMAN S. & SZE V., 2018: *Navion: A Fully Integrated Energy-Efficient Visual-Inertial Odometry Accelerator for Autonomous Navigation of Nano Drones.* .
- SUŠNIK S., KOZMUS P., POKLUKAR J. & MEGLIČ V., 2004: *Molecular characterisation of indigenous Apis mellifera carnica in Slovenia.* *Apidologie* 35/6: 623–636. doi: 10.1051/apido:2004061.
- TANNER D. & VISSCHER K., 2009: *Does the body orientation of waggle dance followers affect the accuracy of recruitment?* *Apidologie* 40/1: 55–62. doi: 10.1051/apido:2008074.
- TAUTZ J., 1996: *Honeybee waggle dance: recruitment success depends on the dance floor.* *Journal of Experimental Biology* 199/6: 1375–1381.
- VADAS R. L., 1994: *The Anatomy of an Ecological Controversy: Honey-Bee Searching Behavior.* *Oikos* 69/1: 158–166. doi: 10.2307/3545297.
- WENNER A. M., 1962: *Sound production during the waggle dance of the honey bee.* *Animal Behaviour* 10/1–2: 79–95. doi: 10.1016/0003-3472(62)90135-5.
- ., 1967: *Honey Bees: Do They Use the Distance Information Contained in Their Dance Maneuver?* *Science* 155/3764: 847–849. doi: 10.1126/science.155.3764.847.
- WENNER A. M., MEADE D. E. & FRIESEN L. J., 1991: *Recruitment, Search Behavior, and Flight Ranges of Honey Bees.* *Integrative and Comparative Biology* 31/6: 768–782. doi: 10.1093/icb/31.6.768.
- WENNER A. M. & WELLS P. H., 1990: *Anatomy of a Controversy: The Question of a "language" Among Bees.* Columbia University Press, 399 p.
- WENNER A. M., WELLS P. H. & JOHNSON D. L., 1969: *Honey Bee Recruitment to Food Sources: Olfaction or Language?* *Science* 164/3875: 84–86. doi: 10.1126/science.164.3875.84.
- WENNER A. M., WELLS P. H. & ROHLF F. J., 1967: *An Analysis of the Waggle Dance and Recruitment in Honey Bees.* *Physiological Zoology* 40/4: 317–344.
- ZEIL J., 1993: *Orientation flights of solitary wasps (Cerceris; Sphecidae; Hymenoptera).* *Journal of Comparative Physiology A* 172/2: 207–222. doi: 10.1007/BF00189397.
- ZELLER M., HELD M., BENDER J., BERZ A., HEINLOTH T., HELLFRITZ T. & PFEIFFER K., 2015: *Transmedulla Neurons in the Sky Compass Network of the Honeybee (Apis mellifera) Are a Possible Site of Circadian Input.* *PLOS ONE* 10/12: e0143244. doi: 10.1371/journal.pone.0143244.