

Betting Blind:

Coping with Uncertainty through Redundancy

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Abstract

Multiple biological groups, such as ant colonies, appear to have a noteworthy inefficiency: they contain vast amounts of redundant members that are not strictly needed to maintain the group. Philosophers and biologists have proposed that such inefficiency is illusory because redundancy enhances the resilience of groups when living under harsh conditions. Still, this proposal is unsatisfactory in different respects. First, it is too vague to account for when redundancy is selectively advantageous. Furthermore, it overlooks cases in which redundancy fails to increase the resilience of groups. This paper offers an account of group redundancy that addresses these difficulties. Specifically, it advances the hypothesis that the mere presence of harsh conditions is not what drives the evolution of redundancy; rather, it is the fact organisms are often unable to predict when they will face harsh conditions. Redundancy enables groups to properly respond to unpredictable circumstances without resorting to the unreliable detection systems of their members. A better understanding of the phenomenon of redundancy is likely to impact other key issues in philosophy of science, including the evolution of cooperation and transitions in individuality, and the role of redundancy in complex systems, be they biological or not.

Keywords redundancy; degeneracy; uncertainty; evolution; cooperation; complex systems.

1 Introduction

Organisms engage in a variety of group behaviors. For example, birds fly in formation and penguins huddle when facing freezing temperatures. The evolutionary explanations for these and other group behaviors often appeal to their efficiency. Birds save energy by placing themselves behind others, and huddling enables organisms to conserve heat (Krause and Ruxton, 2002, §2). Still, several biological groups appear to have a noteworthy inefficiency: they contain vast amounts of redundant members (Charbonneau and Dornhaus, 2015; Birch, 2017). For instance, over half of the workers in ant colonies can be inactive (Charbonneau et al., 2017). In addition to insects, distinct kinds of organisms form groups containing more members than strictly necessary to maintain the group, including microbes (Pedroso, 2018) and mammals (Wilkinson, 1984). But if redundancy is inefficient, why did it evolve and became so widespread in nature?

One way of answering this question is to deny that redundancy is inefficient. In fact, philosophers and biologists have claimed that groups benefit from redundancy when they face ‘harsh environments,’ such as encountering a predator or living through a colder winter than expected (Calcott, 2008; Charbonneau et al., 2017; Pedroso, 2021; Hasegawa et al., 2016).¹ Still, this claim is too broad

¹I chose the expression “harsh environment” because it nicely captures the kind of conditions in which redundant groups might fare better than non-redundant groups. In particular, redundancy likely increases the resilience of groups not only when they face “catastrophic events” (Hasegawa et al., 2016), but also when they cope with less abrupt environmental changes, such as fluctuations in food supply (Charbonneau et al., 2017). Accordingly, the phrase “harsh environment” has the advantage of indicating the presence of a stressor while being agnostic about whether this stressor is a severe disturbance event or not. See Dugatkin (1997) and Pedroso (2021) for related uses of the notion of ‘harsh environment.’

to explain how redundancy evolves. First, harsh conditions are rather common in nature to explain why only certain groups are redundant. Moreover, as I argue later, not every type of redundancy increases the resilience of groups.² My aim with this paper is to enhance our understanding of how redundancy evolves by addressing these difficulties.

One of the central ideas of this paper is that redundancy is an effective strategy for coping with uncertainty. More specifically, redundancy is an inflexible strategy in the sense that it does not utilize environmental cues to adjust its behavior.³ Yet, that is what makes redundancy so effective when organisms face unpredictable environments: groups can properly respond to harsh conditions without resorting to the unreliable detection systems of their members (Section 2). However, this is not the whole story. We cannot arbitrarily increase the resilience of a group by simply adding redundant members to it. In fact, increasing the redundancy of a group can break the group apart (Section 3). Altogether, this paper offers a balanced account of redundancy that takes into account not only its benefits, but also its limitations.

Redundancy is not only a puzzling phenomenon—it is also ubiquitous. A better understanding of the phenomenon of redundancy impacts key issues in philosophy of biology, including the value of optimality models in evolution (Bookstaber and Langsam, 1985; Potochnik, 2017), the evolution of cooperation (Calcott, 2008; Pedroso, 2021), and transitions in individuality (Birch, 2017,

²The observation that redundancy increases the resilience of groups might encourage some readers to think that the theory of group selection is particularly suited for studying redundancy. This might very well be the case. However, an explanation rooted in group selection would have to grapple with the fact that, when redundant groups face harsh conditions, there are winners and losers within the group. Possibly, the theory of group selection could view redundancy as the result of two selective pressures: whereas group-selection would favor redundancy, individual-selection would favor free-riding. Redundancy would thus evolve when group-level selection overrides individual-level selection. For references on group selection, see Okasha (2006) and Bourrat (2021). I thank one of the referees for asking me to clarify this point.

³By contrast, the pitch of avian vocalizations would be an example of a flexible behavior because it changes depending on ambient noise (Stamps, 2016). See Bookstaber and Langsam (1985) for further details on inflexible or coarse strategies.

2012).⁴ Additionally, redundancy is a vital feature of many non-biological systems, including various technologies, institutions, and natural languages (Shannon, 1951; Von Neumann, 1956; Landau, 1969; Bendor, 1985; Gleick, 2012). This suggests that lessons we learn about redundancy in one domain might be valuable to other fields (Wimsatt, 2007; Page, 2010; Taleb, 2012; Charbonneau and Dornhaus, 2015). Indeed, the next section builds upon the literature about redundancy outside of biology to elaborate how redundancy enhances the resilience of groups against harsh environments.

2 The benefits of redundancy

2.1 Redundancy outside of biology

No mechanical equipment is impervious to error. Even jet engines, which are known for being exceptionally reliable, can fail due to a myriad of factors, which includes not only mechanical failures but also unexpected events, such as flocks of geese flying into the turbines. This is partly why aircraft are equipped with redundant engines. In rare cases in which a jet’s engine is lost, as illustrated by the Air France Flight 66 incident in 2017, the crew can rely on the remaining engines to safely land the aircraft (Stewart, 2017). Redundant parts are crucial in engineering because they can prevent the whole system from failing by absorbing errors from its components. Thus, it is far from surprising that redundancy is so prevalent in a wide variety of technologies we depend on, such as energy grids and the World Wide Web (Albert et al., 2000).

Redundancy is a highly effective design strategy because of the following

⁴As we will see, the concepts of redundancy and cooperation are linked because multiple social groups contain “extra” cooperators. The issue of how transitions in individuality evolved can, in turn, be formulated in terms of the problem of cooperation (Bourke, 2011). In particular, Birch (2012) has suggested that the presence of “extra” cooperators might have enabled the evolution of the type of specialization needed for transitions in individuality to occur.

mathematical rule: arithmetic increases in redundancy yield geometric increases in reliability (Landau, 1969). For example, suppose a mechanical device that is not particularly reliable possesses a chance of failure of 40%. If ten of these devices are working in parallel independently, the chance that at least one of them will function properly is approximately 99.99%.⁵ In contrast, consider the reliability of a non-redundant system in which all of the components must function properly: the system’s reliability cannot be higher than its least reliable component. Accordingly, redundancy has the remarkable consequence of enabling systems to be considerably more reliable than any of their components.

So far we have focused on examples of redundancy in engineering. Yet, as some authors have pointed out, redundancy is a valuable strategy for tackling challenges outside of engineering. In particular, the concept of redundancy plays a prominent role in William Wimsatt’s (2007) innovative work on ‘robustness.’ In order to illustrate the connection between redundancy and robustness, consider one of the philosophical topics to which Wimsatt (2007) applies the concept of robustness: the issue of how we should justify our scientific conclusions.

The axiomatic approach is a familiar strategy for structuring scientific theories. According to this approach, a statement is justified because it is either an axiom or a theorem—i.e., it can be derived from the axioms. The axiomatic approach is expected to make scientific theories more reliable by reducing the number of assumptions to which we are committed. However, as Wimsatt (2007) points out, even if no errors are introduced when we select the axioms, the axiomatic approach overlooks the fact that the individuals who derive the theorems are fallible. Specifically, no matter how small the probability of someone making a single derivation mistake is, the probability of correctly deriving a statement approaches zero the higher the number of derivation steps. Because of that,

⁵Provided that ϵ is the chance of error of each component machine, the probability that at least one of the n components will function properly is $1 - \epsilon^n$.

Wimsatt (2007) claims that “[f]allible thinkers should avoid long serial chains of reasoning” (p. 49). As an alternative, he proposes we rely on ‘robust’ theorems which can be derived from multiple or redundant ways. His argument is analogous to the argument for incorporating redundancy in engineering: “[w]ith independent alternative ways of deriving a result, the result is always surer than its weakest derivation” (p. 50). In this respect, Wimsatt proposes we design our theories like many of our artifacts, with built-in redundancy to enhance the reliability of our theories against local errors.⁶

Theorems and pieces of engineering are robust in different ways, however. Robust engineering is what Calcott (2011) calls “robust phenomena” in the sense that it is reliably present despite perturbations and interventions. Accordingly, while theorems are robust due to a particular relation with something in the world, robust phenomena are something in the world itself.⁷ Yet, similar to our scientific theories, evolved systems are also expected to exhibit robust features in order to work reliably under different circumstances (Wimsatt, 2007, pp. 133, 345).⁸ This paper can be thought of as focusing on a particular type of robust phenomena in evolution: the resilience of biological groups against harsh environments. Still, even though the scope of this paper is considerably more modest, it vindicates Wimsatt’s (2007) contention that robustness is a particularly valuable concept to philosophers of science.⁹

⁶It is worth noting that Wimsatt (2007) uses the concept of robustness to tackle a wide range of philosophical topics, such as visual perception, the analytic-synthetic distinction, and the analysis of complex systems. I chose Wimsatt’s criticism of the axiomatic approach because it nicely illustrates how the concepts of robustness and redundancy relate to each other.

⁷Calcott (2011) also distinguishes a third type of robustness in Wimsatt’s (2007) work called “robust detection.” According to it, a result is robust when it can be detected via multiple and independent ways.

⁸In addition to the concept of robustness, another relevant concept in the study of evolution is Wimsatt’s notion of “generative entrenchment.” A generatively entrenched feature is one that “has many things depending on it because it has played a role in generating them” (p. 133), such as the genetic code. Wimsatt views the concepts of robustness and generative entrenchment as complementary measures of “local order” in complex biological systems (p. 355).

⁹I thank one of the reviewers for suggesting me to describe how the topic of this paper fits in

In the next section, I build upon the examples of redundancy discussed previously to make the case that redundancy is an effective evolutionary strategy for biological groups. But in order to show that, I first need to introduce a few concepts.

2.2 From engineering to biology

Life at multiple levels of organization depends on public goods to persist. Public goods are resources shared within a particular group that benefit all of its members (Rankin et al., 2007).¹⁰ There are different types of public goods. Forests and drinking water are examples of essential public goods for humans (Hardin, 1968; Ostrom, 1990). Cancer cells secrete compounds that modify their microenvironment to their advantage (Pepper, 2012; Archetti and Pienta, 2019). Foraging in groups enables individuals to better capture prey and attain information about food patches (Krause and Ruxton, 2002). And the tenacity of bacterial infections is largely due to diffusible molecules they manufacture when they aggregate (Hall-Stoodley et al., 2004; Folkesson et al., 2012).

In order to obtain a valuable public good, groups might need to complete a group-level task (Calcott, 2008). Such tasks are the result of the contribution of multiple individuals. For instance, several pathogenic bacteria secrete iron-binding agents into their local environment called “siderophores” to extract iron from their hosts (Ratledge and Dover, 2000). And multiple army ants build bridges with their own bodies in order to travel over gaps (Anderson

with Wimsatt’s work on robustness. For further work in philosophy of science on robustness, see e.g. Odenbaugh (2006), Mitchell (2009), and Lloyd (2015).

¹⁰Note that this definition of ‘public goods’ differs from other commonly used definitions in the literature. In economics, it is often assumed that public goods are non-excludable in the sense that individuals cannot be barred from consuming the good. The air we breathe is an example of a non-excludable good. In contrast, according to the definition of public goods used in this paper, a resource can be a public good for a group even if members outside of the group are barred from accessing it, such as the spoils of a hunt. Additionally, the definition of ‘public goods’ used in this paper does not assume that the shared resource is costly to produce. See West et al. (2006) for a discussion about public goods in evolution that makes this assumption.

et al., 2002). Yet, one curious feature of several groups is that their tasks are performed by redundant teams.

A group is redundant when it contains more members than typically necessary to complete a particular group task (Birch, 2012; Pedroso, 2021).¹¹ For instance, ant colonies often contain a high proportion of inactive ants that can be recruited to perform a group task, such as foraging or caring for the brood (Charbonneau et al., 2017).¹² And, often times, redundant members are dissimilar from each other even though they contribute to the same group task—e.g., inactive workers within the same colony might become active with distinct probabilities (Hasegawa et al., 2016). That is, the redundant individuals do not have to be replicas of each other.¹³

Nevertheless, redundancy seems wasteful and inefficient in the short-term. But if that is true, why isn’t group redundancy selected against? Philosophers and biologists have proposed that redundancy benefits groups by making them more resilient against harsh conditions (Calcott, 2008; Birch, 2012; Pedroso, 2021; Hasegawa et al., 2016; Charbonneau et al., 2017). For example, a redundant ant colony can replace its workers with its reserve workforce if some of its workers are lost due to, say, a predator attack. As a result, redundancy enables groups to complete vital group tasks, such as foraging and nursing, even if they face hostile conditions.

¹¹Note that, in this paper, the sentence ‘a group is redundant’ does not mean that the group is what is extra but the members *within* the group. Similarly, the expression ‘group redundancy’ will be used in this paper as a convenient abbreviation for redundancy within a particular group as opposed to a collection of groups.

¹²In biology, redundancy is not restricted to social groups. Our body is rife with redundant parts; e.g., humans typically possess two kidneys even though we could survive with only one. Organisms often overproduce zygotes during reproduction (Stearns, 1987; Edelman and Gally, 2001). And multiple genes in the genomes of certain species can perform the same function (Krakauer and Plotkin, 2002; Keller, 2009).

¹³A quick note on terminology. Some authors such as Edelman and Gally (2001) use the term “degeneracy” to refer to cases in which physically different components can perform the same function. They reserve the term “redundancy” to cases in which the elements are copies of each other. In this paper, the term “redundancy” refers to cases in which the extra individuals contribute to the same task, be they copies of each other or not.

Non-biological case	Biological case
System of parallel machines	Group of organisms
System purpose	Group task
Machine error	Failure to complete an individual task due to harsh environments.

Table 1: Translation chart illustrating the connection between the role of redundancy in engineering—as discussed in the previous section—and in biological groups.

Group redundancy thus functions as a fail-safe mechanism. As we have seen previously, redundancy plays a similar role in engineering. One key difference though is that, in the biological case, the focus is on component failures due to harsh conditions, such as predator attacks and cold winters (Table 1).¹⁴ Still, the main insight remains the same. In both engineering and biology, redundancy enables a system to complete a task even if some of its components fails. And, most importantly, introducing redundancy can dramatically increase the resilience of a system even when its components are prone to failure.

Nevertheless, the fact that redundancy functions as a fail-safe mechanism falls short of explaining how redundant groups evolve. Harsh conditions are rather common in nature to explain why only certain groups are redundant. Accordingly, we still need to specify the kind of selective environment that favors redundancy. That is the topic of the next section.

2.3 How redundant groups cope with uncertainty

Organisms often find themselves in what Kim Sterelny (2003) calls *informationally opaque* environments. In such environments, organisms fail to properly track features about their environment that might affect their fitness, such as food and predators. This happens largely because extracting and processing in-

¹⁴This is not to say that groups only fail to perform group tasks due to harsh environments. Groups can also fail to perform a task because their members are not well-matched to the task at hand.

formation incurs metabolic costs (Marzen and DeDeo, 2017; Flack et al., 2013). Moreover, the living world has no shortage of clever tactics aimed at misleading other organisms (Sterelny, 2003; Dawkins, 1982; Trivers, 2011). Sexual mimicry is a case in point. For example, female fireflies of the species *Photuris versicolor* prey on males from other species of firefly by mimicking the flash responses of the prey’s females (Lloyd, 1975). Many organisms are also particularly skilled at concealing crucial information from others. When the mantis shrimp become defenseless while molting, they might “bluff” by putting on a threat display in order to deter intruders from stealing the cavities they live in (Adams and Caldwell, 1990). Moreover, a previously effective detection system might be compromised by an abrupt change in the abiotic environment.¹⁵ For instance, multiple migratory birds rely on day length for deciding when to migrate. Yet, due to climate change, day length has become an unreliable cue for migratory birds, such as flycatchers (Both et al., 2006).¹⁶

In response to opaque environments, lineages may acquire more accurate detection systems in order to improve their ability to detect specific cues (Sterelny, 2003). For example, organisms within a lineage might improve their visual acuity (Caves et al., 2018), or inspect predators to better assess their risks (Pitcher et al., 1986). Alternatively, as migratory species illustrate, organisms can rely on multiple cues for navigation, including celestial and magnetic information (Gould, 1998). Organisms also modify their environments to make it less informationally opaque. Ants can, for instance, secrete pheromones to create trails

¹⁵Although environments can be opaque due to nonliving features in the environment, such as features in the terrain, “biological agents pose far more difficult epistemic problems. An animal’s predators, prey, and competitors *are* under selection to sabotage its actions” (Sterelny, 2003, p. 25).

¹⁶Day length has become an unreliable cue for certain species because species across the trophic levels respond differently to climate change. In the case of the flycatcher species *Ficedula hypoleuca*, Both et al. (2006) provide evidence that climate change induced a mistiming between their breeding time and the peak in food abundance. This example illustrates how opacity can affect survival when environmental changes are too rapid for organisms to evolve the necessary adaptations via natural selection.

to food sources with higher profitability (Jackson and Ratnieks, 2006). Finally, organisms can acquire accurate information about their environments through learning (Skyrms, 2010). All in all, these different types of adaptations make the environment less opaque by enhancing the quality of information organisms extract from the environment. Yet, redundancy offers an alternative kind of strategy for coping with opaque environments.

As an example, consider the feeding behavior of common vampire bats (*Desmodus rotundus*). They feed on blood and can only survive for approximately three days without it (McNab, 1973). Yet, vampire bats often fail to obtain blood during their feeding trips. For example, Wilkinson (1984) reports that, at one study site in Costa Rica, 86 of 477 bats failed to feed on 31 nights. The feeding behavior of vampire bats thus faces an opaque environment in which failures are not only recurrent but also consequential for their fitness.

Common vampire bats rely on redundancy in order obtain enough blood to survive. Specifically, common vampire bats form coalitions in which they share the acquired blood with their fellow members. In this way, individual failure does not necessarily compromise the ability of the group to obtain enough blood to survive (Wilkinson, 1984; Carter and Wilkinson, 2013). The blood-sharing behavior in vampire bats illustrates how redundancy enables groups to obtain a valuable public good in an opaque environment: (i) multiple individuals perform the same task (e.g., hunting); and (ii) since the chance of failure is significant, having a surplus of individuals that can perform the same task increases the chance that the group will obtain enough of the public good to survive (e.g., blood).

Redundancy is an ‘inflexible’ strategy—i.e., it does not utilize environmental cues to adjust its behavior (Bookstaber and Langsam, 1985). Yet, that is what makes redundancy so effective when organisms face opaque environments. Flex-

ible strategies are powerless when detection errors are common. For example, a red warbler that expels cuckoo chicks from its nest risks never raising its own chicks if it systematically commits discrimination errors (Sterelny, 2003, pp. 12-13). In contrast, as the vampire bat example illustrates, redundancy increases the chance that vital group tasks are successfully performed without requiring organisms to accurately track harsh conditions. In other words, redundancy by itself does not reduce the chance of errors from occurring—e.g., a frustrated hunting trip. Rather, it reduces the cost of errors relative to non-redundant groups.¹⁷

So far we have focused on the benefits of group redundancy in relation to non-redundant groups. As we have seen, redundancy is particularly beneficial when organisms cope with informationally opaque environments. The mere presence of harsh conditions is not what drives the evolution of redundancy; instead, it is the fact that groups often fail to predict when they will face a run of bad luck. Alas, as we will see in the next section, we cannot arbitrarily increase the resilience of a group by adding redundancy to it.

3 The limits of redundancy

Redundancy is not free. In particular, maintaining redundant members can incur costs to the other members of the group.¹⁸ Such costs can make redundancy disadvantageous in ‘transparent environments,’ where organisms can properly track features of their environment. For instance, if future disturbances are not expected, expelling the redundant members from the group appears to be

¹⁷There is a close parallel with Taleb’s (2007) approach to uncertainty. According to him, for domains in which humans are particularly bad at predicting outlier events such as financial markets, we should concentrate on minimizing the damage due to outlier events instead of attempting to improve our predictive power.

¹⁸These costs can take multiple forms, including increase of competition for resources (e.g., food, mates, nest sites), higher rates of disease transmission facilitated by close proximity, or higher visibility to predators due to an increase in group size.

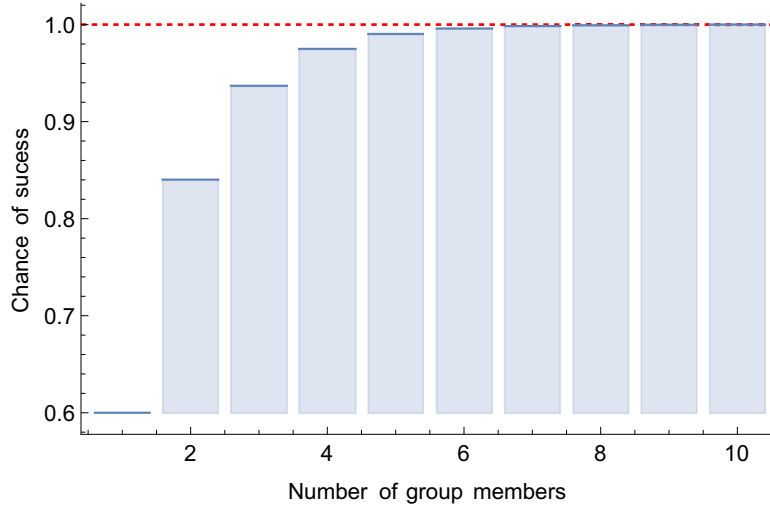


Figure 1: Plot of the success of completing a group task versus the number of group members. The chance of completing the group task is equal to $1 - 0.4^n$, where n is the number of group members.

a cost-effective strategy. The situation is different in opaque environments because the benefits of redundancy might outweigh its costs. That is, the costs of having extra members is offset by the benefits of completing a vital group task, such as foraging.

However, if redundancy is so beneficial under opaque environments, why aren't groups more redundant than they actually are? One of the reasons is the gains in benefits due to redundancy diminish as the number of redundant members increases. To illustrate that, consider the case in which each group member has a success rate of 60% and, as a result, only one member is strictly necessary to complete the task (Figure 1). Note that adding a single redundant member dramatically increases the chance of completing a group task (from 60% to 84%). Nonetheless, the gains due to redundancy rapidly decline with the number of redundant members. As I elaborate later, there must be a point after which redundancy becomes disadvantageous because the costs of adding a new redundant member are higher than the gained benefit.

Still, the above example relies on the simplifying assumption that the chance of failure of each group member is independent from each other. As we will see next, the returns due to redundancy can vanish once we abandon this assumption.

3.1 Coupling reduces the benefits of redundancy

Redundancy can also make technologies less reliable. As the sociologist Charles Perrow (2011) points out, adding redundancy to nuclear plants and other high-risk technologies increases the complexity of the system and, as a result, amplifies the chance of system failure due to unexpected interactions between the system components. For example, although adding redundant engines might increase the resilience of the aircraft against engine failures, it also increases the chance of fires that might destroy the whole aircraft (Sagan, 2004). Because of this, two engines might produce a net benefit but not three or more.¹⁹

In general terms, the benefit due to redundancy depends on how error propagates in the system. Redundancy increases the reliability of a system insofar as the chance of failures of the redundant components is statistically independent to a certain degree.²⁰ In other words, the redundant components should be *decoupled*. The reason is that the benefit of having extra components disappears if component failures easily percolate through the system. Hence, the impact of component failures must be contained for redundancy to enhance the reliability of the whole system.

¹⁹A similar remark applies to redundancy within organisms. For example, adding extra appendages to an organism might diminish its survival if it dramatically increases the chance of debilitating injuries.

²⁰Authors working on different types of redundancy have drawn attention to the value of independence in redundant systems. Bendor (1985) argues that the redundant teams within institutions should be independent. In the debate over robustness analysis, Pirtle et al. (2018) make the case for the importance of independent models in studying engineering systems. Additionally, it is reasonable to assume that the redundant parts within an organisms should also be decoupled. For example, octopuses possess multiple arms that regenerate independently (Fossati et al., 2013). Without the ability to fail independently, a damaged or lost arm in an octopus would compromise the whole organism.

In order to elaborate the role of decoupling for group tasks, consider two vampire bats that are equally skilled at blood-hunting.²¹ Call them “Maria” and “Pedro.” Suppose that Maria and Pedro form a redundant group in the sense that only one of them needs to hunt successfully on any particular night to obtain enough blood for both of them to survive. Decoupling—and coupling—among the redundant members of a group comes in degrees. The highest level of decoupling for Maria and Pedro occurs when their chances of being successful in their hunt are independent; i.e., when the success or failure of Maria during her hunt does not affect the chance that Pedro is successful, and vice-versa. Conversely, the level of coupling between Maria and Pedro increases with the extent by which the success of one of them increases the chance that the other one will also be successful in the hunt.

To make this example more precise, we can formulate the level of coupling between Maria and Pedro in terms of conditional probabilities.²² To simplify the notation, assume that ‘M’ and ‘P’ refer to Maria and Pedro, respectively. Let h_i be the proposition that the bat i hunts successfully, where $i \in \{M, P\}$. Each bat i hunts successfully with probability $P(h_i)$ and unsuccessful with probability $P(\neg h_i) = 1 - P(h_i)$. Further, Maria and Pedro have the same chance a of being successful in their hunt (i.e., their hunting skills are equivalent):

$$P(h_i) = a, \quad \text{for all } i. \quad (1)$$

With coupling, the success of one of the bats increases the chance that the other

²¹The two vampire bats are assumed to be equally skilled at hunting because this example focuses on how redundancy—rather differences in skill—affects the chance of group task completion.

²²Jonathan Bendor (1985) uses a similar example to argue for the value of redundancy in human organizations.

one is also successful:

$$P(h_M | h_P) = P(h_P | h_M) > a.^{23} \quad (2)$$

Accordingly, if one of the bats is successful in the hunt, the probability that the other bat is successful increases with the level of coupling.

Decoupling is highly beneficial for the group formed by Maria and Pedro. To understand why, consider the following turn of events. Suppose Pedro was successful. In this case, it is irrelevant whether Maria also succeeds. The reason for this is because, by hypothesis, only one of the them needs to be successful for the group to obtain enough food to survive. Now suppose Pedro was unlucky and failed to obtain any blood this time around. In this case, Maria must be successful for the group to survive. However, provided that Pedro fails, the probability that Maria will also fail increases with coupling. The reason for this is that coupling increases not only the chance of joint successes, but also of joint failures. In other words, since the chance of failure is significant, the success of Maria and Pedro as a group depends on the probability that *only* one of them is successful. But that is exactly the probability that coupling decreases. Maria and Pedro are thus better off as a group if their chance of being successful is as independent as possible (see Appendix A for a formal version of this argument).

The above example involving Maria and Pedro is fairly general. The group members do not have to be bats, but any type of organism that performs a group task together. Moreover, the above argument can be extended to redundant groups with more than two members by applying the same line of reasoning to any arbitrary pair of individuals in the group. More specifically, provided that only one member of a redundant group needs to be successful, coupling

²³These two conditional probabilities have the same value because the unconditional probabilities are equal—i.e., Eq. (1). Specifically, $P(h_M | h_P) = P(h_M \wedge h_P)/a = P(h_P \wedge h_M)/a = P(h_P | h_M)$.

between any pair of members of this group will increase the chance of joint failure. Accordingly, even in the case of redundant groups with more than two members, decoupling ensures that the redundant members of a group can better prevent local failures from spreading to the remaining redundant members.²⁴

Still, it is worth noting that the above example focuses on an idealized case of redundancy. In particular, it is assumed that individuals possess the same skill level, and that joint successes produce the exact same payoff as individual successes. Nevertheless, the goal of this example is not to offer a detailed description of a particular redundant group in nature, but to offer a straightforward case to study how coupling affects redundant groups. Specifically, the above example aimed to show how redundancy is ineffective if the redundant members are highly coupled.

3.2 High levels of redundancy promote free-riders

Biological groups benefit from their redundancy at the expense of their redundant members. For example, redundant ant colonies increase their resilience because dead workers can be replaced by other workers from their reserve forces. The redundant workers in this example can be thought of as ‘cooperators:’ they bear the costs of the group’s increased resilience while providing a benefit to the whole group.²⁵ Accordingly, in terms of social evolution, biological groups are redundant if they contain more cooperators than strictly necessary for task completion (Birch, 2012, 2017).

However, in highly redundant groups such as insect colonies, the expected

²⁴Note that decoupling is detrimental when redundancy is absent, however. For example, suppose that Maria and Pedro must both succeed in their hunts to obtain enough blood to survive. In this case, coupling is desirable because it increases the probability of joint success.

²⁵In social evolutionary biology, cooperative behaviors are understood as interactions between individuals that benefit the recipient but not necessarily the performer of the behavior. Note that this definition of cooperation abstracts away specific biological details of the involved organisms, including their genetics and modes of reproduction (Calcott, 2008). Yet, as will be discussed, the specific biological details are key for understanding how cooperation might evolve.

gain from being a cooperator as opposed to a free-rider seems negligible:

When redundancy is extreme, the contribution of any given individual to the probability of task success is extremely small. The result is that, as long as the cost attached to participating is significant, apathy will yield a higher expected payoff than participation even when the potential benefits of task completion are large (Birch, 2012, p. 374).

Essentially, group redundancy exacerbates the free-rider problem because the incentive to free-ride increases with the presence of extra cooperators. High levels of redundancy thus appear to be evolutionarily unstable. Yet, as insect colonies illustrate, nature is rife with redundant groups.

One approach for solving the puzzle posed by redundancy is to include the ‘indirect benefits’ of cooperating due to genetic relatedness. That is because the cost of being a cooperator in redundant groups might be offset by the indirect benefits conferred to other individuals carrying the same gene. This approach seems particularly suited to account for redundancy in insect colonies because of their high level of genetic relatedness (Wilson and Sober, 1989; Birch, 2017). Still, kinship alone is not sufficient to prevent conflict within insect colonies. For example, due to how sex allocation works in some hymenopteran colonies, male production can be a source of conflict within such colonies because workers are more closely related to their sons than to the queen’s sons (Ratnieks et al., 2006). Moreover, costly cooperation becomes unstable within a population if the indirect benefit for cooperating—i.e., the benefit weighed by genetic relatedness—is lower than the cost of cooperating.²⁶ Accordingly, one of the stumbling blocks for explaining redundancy in terms of kin selection is that we

²⁶This point is nicely summarized by a well-known version of Hamilton’s rule according to which selection will favor a costly behavior if $r \times b > c$, where c is the cost of the behavior to the actor, b is the benefit to the recipient, and r is the genetic relatedness between the actor and the recipient.

need to show that the indirect benefit for cooperating is higher than its cost.

As Birch (2012) points out, the expected indirect benefit of cooperating seems negligible in comparison to its direct costs within highly redundant groups.²⁷ That is because, in a highly redundant group, the contribution of a single individual for completing a task is still minuscule and, consequently, so is the direct and indirect benefits of cooperating relative to its costs.²⁸ To solve this puzzle, Birch (2012) advances the hypothesis that high levels of redundancy within insect colonies can be evolutionary stable due to within-group coercion. His hypothesis is motivated by empirical studies of coercive behaviors in insect colonies, such as the presence of workers that eat the eggs laid by other workers but not by the queen (Ratnieks and Wenseleers, 2008).²⁹ His reasoning is that coercion makes free-riding more costly which, in turn, makes cooperation more likely to evolve within redundant groups. In other words, Birch claims that the presence of systematic coercion facilitated the evolution of extreme redundancy. However, Birch (2012) does not deny the importance of kinship in the evolution of redundancy within insect colonies. Rather, his hypothesis is that kinship first led to the evolution of coercive behaviors, which then enabled the evolution of extreme redundancy.³⁰

Unlike Birch’s (2012) hypothesis, Pedroso (2021) has recently proposed that redundancy can be stable in the absence of coercion. In his view, redundancy

²⁷Birch (2012) draws a parallel with the ‘paradox of voting’ in order to make the puzzle posed by redundancy more vivid. In regards to voting, the puzzle is that people vote in large numbers even though a single vote is unlikely to change the outcome of an election. Accordingly, similar to redundancy, the expected benefits of voting is negligible relative to the costs of voting.

²⁸Additionally, the level of genetic relatedness in some insect colonies seems too low to maintain altruistic behaviors without them being socially enforced (Ratnieks and Wenseleers, 2008).

²⁹The term ‘coercion’ is used here as a technical term to cover a variety of social interactions that promote altruism within the group, such as the policing behavior of worker bees. Ratnieks and Wenseleers (2008) characterize coercion as any type of ‘social pressure’ that tends to prevent individuals from harming the group by acting selfishly. Accordingly, like the policing behavior of worker bees, retaliatory aggression in animal societies (Clutton-Brock and Parker, 1995) and altruistic punishment in humans (Fehr and Gächter, 2002; Boyd et al., 2003) might also be thought of as examples of coercion.

³⁰See Birch (2012, Fig. 4) for a summary of his hypothesis.

can evolve without coercion if the group members are behind a ‘Darwinian veil of ignorance,’ in the sense that they have to decide whether they will cooperate in the absence of information about the strategies adopted by the other group members. His reasoning is that, because of the Darwinian veil of ignorance, group members face the uncertainty of not having enough cooperators to attain a vital group benefit, such as protection against predators. Because of this, individuals are expected to bet on cooperating with a certain probability. Moreover, the higher the benefit produced by the group task, the higher the incentive to bet on cooperating.³¹ Pedroso’s (2021) hypothesis is that, when individuals highly benefit from a group task, extra cooperators can evolve when group members are ignorant about the strategies of others.

My goal in reviewing the literature on redundant cooperators is not to offer a particular solution to this debate. Rather, my point is to emphasize that high levels of redundancy are only evolutionarily stable under specific conditions. Group redundancy might require individuals that are capable of punishing non-cooperators (Birch, 2012), or that are ignorant about the strategies of the other members (Pedroso, 2021). Accordingly, by formulating group redundancy in terms of social evolution, it becomes evident that redundancy might be short-lived. That is, in the absence of a mechanism that restrains the evolution of free-riders, extreme redundancy is likely to be wiped out by selection.

Altogether, the main take-home message of this section is that redundancy is limited in its ability to increase the resilience of groups against harsh conditions. First, the gains due to redundancy face diminishing returns as the number of redundant members increase. Accordingly, once we factor in the costs of adding redundant members to the group, there must be a point after which adding

³¹Group tasks in Pedroso’s (2021) account are modeled as a type of public goods game called “Threshold Games.” Unlike the Prisoner’s Dilemma, players in a Threshold Game obtain a benefit only if enough members of the group cooperate. See Archetti and Scheuring (2012) and Bach et al. (2006) for further details on threshold games.

redundant members harms the group. Further, the benefits due to redundant components vanish if the redundant components are highly coupled. That is, adding extra members is not sufficient to increase the resilience of the group; tasks should also be allocated in such a way that the redundant members can fail independently. Finally, high levels of redundancy increase the incentive of group members to free-ride. As a result, high levels of redundancy risk being evolutionarily unstable due to the proliferation of free-riders.

4 Conclusion

Nature is replete with redundant groups that contain more members than strictly needed to perform vital group tasks, such as foraging and nursing. Yet, redundancy is not free. At the least, having redundant members depletes extra resources from the group. Hence, the main challenge is to specify the circumstances in which redundancy yields a net benefit. One of the main ideas of this paper is that redundancy is particularly beneficial when groups face ‘opaque environments.’ In such environments, organisms utilize detection systems that are ill-matched with the level of complexity of their environment. Redundancy fares well in opaque environments because it contains the impact of errors instead of preventing such errors from occurring. In this way, redundant groups can properly cope with a wide range of unexpected harsh conditions without relying on the faulty detection systems of their members. Still, the benefits of redundancy are contingent upon certain group features. First, the redundant members should be decoupled because, otherwise, redundancy would be powerless against hostile conditions. Moreover, high levels of redundancy become evolutionarily unstable in the absence of evolutionary mechanisms capable of suppressing free-riders. Accordingly, biological groups cannot arbitrarily increase their resilience to harsh environments by simply augmenting their redundant workforce.

In addition to being a curious feature about life on Earth, the phenomenon of redundancy offers a fresh perspective on key topics in philosophy of science. Specifically, the evolution of ‘redundant cooperators’ raises an exacerbated version of the problem of cooperation because individuals possess a higher incentive to free-ride in the presence of extra cooperators (Birch, 2012; Pedroso, 2021). Regarding the topic of scientific explanation, redundancy challenges the adequacy of optimality models for studying evolution (Hasegawa et al., 2016; Potochnik, 2017). Finally, the fact that redundancy is a ubiquitous feature in biological and non-biological systems underscores the value of the concept of ‘robustness’ in philosophy and the sciences (Wimsatt, 2007; Calcott, 2011). Thus, the concept of redundancy is useful not only for formulating and assessing hypotheses on evolution, but also for identifying principles shared across disciplines.

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References

- E. Adams and R. Caldwell. Deceptive communication in asymmetric fights of the stomatopod crustacean *Gonodactylus bredini*. *Animal Behaviour*, 39(4): 706–716, 1990.

- R. Albert, H. Jeong, and A. Barabási. Error and attack tolerance of complex networks. *Nature*, 406(6794):378, 2000.
- C. Anderson, G. Theraulaz, and J-L. Deneubourg. Self-assemblages in insect societies. *Insectes Sociaux*, 49:99–110, 2002.
- M. Archetti and K. Pienta. Cooperation among cancer cells: applying game theory to cancer. *Nature Reviews Cancer*, 19(2):110–117, 2019.
- M. Archetti and I. Scheuring. Game theory of public goods in one-shot social dilemmas without assortment. *Journal of Theoretical Biology*, 299:9–20, 2012.
- L. Bach, T. Helvik, and F. Christiansen. The evolution of n-player cooperation—threshold games and ESS bifurcations. *Journal of Theoretical Biology*, 238:426–434, 2006.
- J. Bendor. *Parallel Systems: Redundancy in government*. University of California Press, 1985.
- J. Birch. Collective action in the fraternal transitions. *Biology and Philosophy*, 27:363–380, 2012.
- J. Birch. *The Philosophy of Social Evolution*. Oxford University Press, 2017.
- R. Bookstaber and J. Langsam. On the optimality of coarse behavior rules. *Journal of Theoretical Biology*, 116(2):161–193, 1985.
- C. Both, S. Bouwhuis, C. Lessells, and M. Visser. Climate change and population declines in a long-distance migratory bird. *Nature*, 441(7089):81, 2006.
- A Bourke. *Principles of Social Evolution*. Oxford University Press, 2011.
- P. Bourrat. *Facts, Conventions, and the Levels of Selection*. Cambridge University Press, Cambridge, 2021.

- R. Boyd, H. Gintis, S. Bowles, and P. Richerson. The evolution of altruistic punishment. *Proceedings of the National Academy of Sciences*, 100(6):3531–3535, 2003.
- B. Calcott. The other cooperation problem: Generating benefit. *Biology & Philosophy*, 23:179–203, 2008.
- B. Calcott. Wimsatt and the robustness family: Review of wimsatt’s re-engineering philosophy for limited beings. *Biology & Philosophy*, 26:281–293, 2011.
- G. Carter and G. Wilkinson. Food sharing in vampire bats: reciprocal help predicts donations more than relatedness or harassment. *Proceedings of the Royal Society B: Biological Sciences*, 280:20122573, 2013.
- E. Caves, N. Brandley, and S. Johnsen. Visual acuity and the evolution of signals. *Trends in Ecology & Evolution*, 33(5):358–372, 2018.
- D. Charbonneau and A. Dornhaus. When doing nothing is something: How task allocation strategies compromise between flexibility, efficiency, and inactive agents. *Journal of Bioeconomics*, 17:217–242, 2015.
- D. Charbonneau, T. Sasaki, and A. Dornhaus. Who needs ‘lazy’ workers? Inactive workers act as a ‘reserve’ labor force replacing active workers, but inactive workers are not replaced when they are removed. *PLoS ONE*, 12:e0184074, 2017.
- T. Clutton-Brock and G. Parker. Punishment in animal societies. *Nature*, 373:209–216, 1995.
- R. Dawkins. *The Extended Phenotype*. Oxford University Press, Oxford, 1982.
- L. Dugatkin. *Cooperation Among Animals: An Evolutionary Perspective*. Oxford University Press, 1997.

- G. Edelman and J. Gally. Degeneracy and complexity in biological systems. *Proceedings of the National Academy of Sciences*, 98(24):13763–13768, 2001.
- E. Fehr and S. Gächter. Altruistic punishment in humans. *Nature*, 415:137–140, 2002.
- J. Flack, D. Erwin, T. Elliot, and D. Krakauer. Timescales, symmetry, and uncertainty reduction in the origins of hierarchy in biological systems. In K. Sterelny, R. Joyce, B. Calcott, and B. Fraser, editors, *Evolution Cooperation and Complexity*, pages 45–74. MIT Press, 2013.
- A. Folkesson, L. Jelsbak, L. Yang, H. Johansen, O. Ciofu, N. Høiby, and S. Molin. Adaptation of pseudomonas aeruginosa to the cystic fibrosis airway: an evolutionary perspective. *Nature Reviews Microbiology*, 10(12):841–851, 2012.
- S. Fossati, F. Carella, G. De Vico, F. Benfenati, and L. Zullo. Octopus arm regeneration: role of acetylcholinesterase during morphological modification. *Journal of Experimental Marine Biology and Ecology*, 447:93–99, 2013.
- J. Gleick. *The Information: A history, a theory, a flood*. Vintage, 2012.
- J. Gould. Sensory bases of navigation. *Current Biology*, 8(20):R731–R738, 1998.
- L Hall-Stoodley, J Costerton, and P Stoodley. Bacterial biofilms: from the natural environment to infectious diseases. *Nature Reviews Microbiology*, 2: 95–108, 2004.
- G. Hardin. The tragedy of the commons. *Science*, 162:1243–1248, 1968.
- E. Hasegawa, Y. Ishii, K. Tada, K. Kobayashi, and J. Yoshimura. Lazy workers are necessary for long-term sustainability in insect societies. *Scientific Reports*, 6(1):1–9, 2016.

- D. Jackson and F. Ratnieks. Communication in ants. *Current Biology*, 16(15): R570–R574, 2006.
- E. Keller. *The Century of the Gene*. Harvard University Press, 2009.
- D. Krakauer and J. Plotkin. Redundancy, antiredundancy, and the robustness of genomes. *Proceedings of the National Academy of Sciences*, 99:1405–1409, 2002.
- J. Krause and G. Ruxton. *Living in Groups*. Oxford University Press, 2002.
- M. Landau. Redundancy, rationality, and the problem of duplication and overlap. *Public Administration Review*, 29(4):346–358, 1969.
- E. Lloyd. Model robustness as a confirmatory virtue: The case of climate science. *Studies in History and Philosophy of Science Part A*, 49:58–68, 2015.
- J. Lloyd. Aggressive mimicry in photuris fireflies: Signal repertoires by femmes fatales. *Science*, 187(4175):452–453, 1975.
- S. Marzen and S. DeDeo. The evolution of lossy compression. *Journal of The Royal Society Interface*, 14, 2017.
- B. McNab. Energetics and the distribution of vampires. *Journal of Mammalogy*, 54(1):131–144, 1973.
- S. Mitchell. *Unsimple truths: Science, complexity, and policy*. University of Chicago Press, 2009.
- J. Odenbaugh. The strategy of “the strategy of model building in population biology”. *Biology and Philosophy*, 21:607–621, 2006.
- S. Okasha. *Evolution and the Levels of Selection*. Oxford University Press, Oxford, 2006.

- E. Ostrom. *Governing the Commons: The evolution of institutions for collective action*. Cambridge University Press, 1990.
- S. Page. *Diversity and Complexity*. Princeton University Press, 2010.
- M. Pedroso. The impact of population bottlenecks on the social lives of microbes. *Biological Theory*, 13:190–198, 2018.
- M. Pedroso. Blind cooperation: The evolution of redundancy via ignorance. *The British Journal for the Philosophy of Science*, 2021.
- J. Pepper. Drugs that target pathogen public goods are robust against evolved drug resistance. *Evolutionary Applications*, 5(7):757–761, 2012.
- C. Perrow. *Normal Accidents: Living with high risk technologies*. Princeton University Press, 2011.
- Z. Pirtle, J. Odenbaugh, A. Hamilton, and Z. Szajnfarder. Engineering model independence: A strategy to encourage independence among models. *Techné: Research in Philosophy and Technology*, 22:191–229, 2018.
- T. Pitcher, D. Green, and A. Magurran. Dicing with death: Predator inspection behaviour in minnow shoals. *Journal of Fish Biology*, 28(4):439–448, 1986.
- A. Potochnik. *Idealization and the Aims of Science*. University of Chicago Press, 2017.
- D. Rankin, K. Bargum, and H. Kokko. The tragedy of the commons in evolutionary biology. *Trends in Ecology & Evolution*, 22:643–651, 2007.
- C. Ratledge and L. Dover. Iron metabolism in pathogenic bacteria. *Annual Reviews in Microbiology*, 54(1):881–941, 2000.
- F. Ratnieks and T. Wenseleers. Altruism in insect societies and beyond: voluntary or enforced? *Trends in Ecology & Evolution*, 23:45–52, 2008.

- F. Ratnieks, K. Foster, and T. Wenseleers. Conflict resolution in insect societies. *Annual Review of Entomology*, 51:581–608, 2006.
- S. Sagan. The problem of redundancy problem: Why more nuclear security forces may produce less nuclear security. *Risk Analysis: An International Journal*, 24(4):935–946, 2004.
- C. Shannon. Prediction and entropy of printed english. *Bell System Technical Journal*, 30(1):50–64, 1951.
- B. Skyrms. *Signals: Evolution, learning, and information*. Oxford University Press, 2010.
- J. Stamps. Individual differences in behavioural plasticities. *Biological Reviews*, 91(2):534–567, 2016.
- S. Stearns. The selection-arena hypothesis. In S. Stearns, editor, *The Evolution of Sex and its Consequences*, pages 337–349. Springer, 1987.
- K. Sterelny. *Thought in a Hostile World: The evolution of human cognition*. Wiley-Blackwell, 2003.
- J. Stewart. How air france will rescue its A380 with a shattered engine. *Wired*, 2017. URL <https://www.wired.com/story/how-air-france-will-rescue-its-a380-with-a-shattered-engine/>.
- N. Taleb. *The Black Swan: The impact of the highly improbable*. Random house, 2007.
- N. Taleb. *Antifragile: How to live in a world we don't understand*. Allen Lane London, 2012.
- R. Trivers. *The Folly of Fools: The logic of deceit and self-deception in human life*. Basic Books, 2011.

- J. Von Neumann. Probabilistic logics and the synthesis of reliable organisms from unreliable components. In C. Shannon and J. McCarthy, editors, *Automata Studies*, pages 43–98. Princeton University Press, 1956.
- S. West, A. Griffin, A. Gardner, and S. Diggle. Social evolution theory of microorganisms. *Nature Reviews Microbiology*, 4:597–607, 2006.
- G. Wilkinson. Reciprocal food sharing in the vampire bat. *Nature*, 308:181–184, 1984.
- D. Wilson and E. Sober. Reviving the superorganism. *Journal of Theoretical Biology*, 136:337–356, 1989.
- W. Wimsatt. *Re-Engineering Philosophy for Limited Beings: Piecewise Approximations to Reality*. Harvard University Press, Cambridge, 2007.

A How coupling affects group redundancy (formal version)

The goal of this appendix is to offer a formal version of the explanation presented in Section 3.1 that coupling diminishes the benefits of redundancy. As before, Maria and Pedro have the same chance a of being successful—i.e., $P(h_i) = a$ for $i \in \{M, P\}$. And, with coupling, the conditional probabilities $P(h_M | h_P)$ and $P(h_P | h_M)$ become strictly higher than a .

The group formed by Maria and Pedro has a probability $P(h_M \vee h_P)$ of being successful. The chance that Maria and Pedro will be jointly successful increases with coupling because, by definition, $P(h_M \wedge h_P) = P(h_M | h_P) \cdot a$. Additionally, $P(h_M \vee h_P) = 2a - P(h_M \wedge h_P)$. Therefore, since a is a constant, the probability that the group is successful decreases with coupling.

Coupling reduces the chance that Maria or Pedro are successful because it increases the probability of joint failures, $P(\neg h_M \wedge \neg h_P)$. In order to show that, consider the following two instances of the law of total probability:

$$\begin{aligned} P(h_M \wedge h_P) + P(\neg h_M \wedge h_P) &= P(h_P) = a, \\ P(\neg h_M \wedge h_P) + P(\neg h_M \wedge \neg h_P) &= P(\neg h_M) = 1 - a. \end{aligned} \tag{3}$$

Since a is a constant, it follows from Eq. (3) that increasing $P(h_M \wedge h_P)$ decreases the value of $P(\neg h_M \wedge h_P)$ which, in turn, increases the value of $P(\neg h_M \wedge \neg h_P)$. Therefore, the chance of joint failures increases with coupling.